TROPHIC STATUS, HABITAT USE

AND CLIMATE CHANGE IMPACTS

ON AVIAN SPECIES OF COASTAL GEORGIA.

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This dissertation is dedicated to my wife, Erin, for love, support and patience through this process, and to my grandfather, Paul Hunter, for inspiring my curiosity about all things natural.

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Dissertation: Trophic status, habitat use and climate change impacts on avian species of coastal Georgia.

ABSTRACT.--- Plant, invertebrate and feather $\delta^{13}C$ and $\delta^{15}N$ stable isotopic signatures were used to trace avian plant production sources and prey items in five habitats of coastal Georgia: tidal forest, oak forest, pine forest, shrub and saltmarsh. *Isosource* 1.3.1 mixing models of plant production sources were successful on Sapelo Island where there were large differences in photosynthetic pathways and hydrology, but failed in the Clayhole Swamp. Model sensitivity analysis indicated that the trophic position was the most important parameter to know for partitioning plant production sources and isotopic enrichment of $\delta^{13}C$ and $\delta^{15}N$ in birds were equally important in determining prey items. Painted Buntings, the species of highest concern in the region, were almost as dependent on saltmarsh vegetation as they were on shrub and forest vegetation (~40%). Greater dependence of young of year Yellow-throated Warblers, White-eyed Vireos and Brown-headed Nuthatches on C_3 saltmarsh vegetation suggests the saltmarsh may be providing an important source of protein for nestling birds across all habitats on Sapelo Island. Avian conservation efforts in coastal Georgia should include nearby saltmarsh to provide not only the necessary food resources for shrub-associated species, but also for forest interior species during the breeding season.

Estimated habitat changes for 2100 due to climate change induced sea-level rise and coastal development indicate that sea-level rise is the greatest threat to saltmarsh and coastal shrub habitat, whereas accelerated urban development is the greatest threat to oak and pine forests. Tidal forests may serve as important refuges for closed-canopy species, such as Northern Parula, that will lose their preferred oak and pine habitats.

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BREEDING DENSITIES AND HABITAT RELATIONSHIPS OF AVIAN SPECIES IN COASTAL GEORGIA, USA, USING DISTANCE-SAMPLING AND INDICATOR SPECIES ANALYSIS

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Abstract. Avian conservation requires understanding species-habitat relationships and accurate estimates of population parameters, such as density and size, within each habitat type. Distance-sampling methods may accurately estimate population densities, while multivariate techniques, such as Indicator Species Analysis and Canonical Correspondence Analysis, assess species-habitat relationships. Avian breeding bird densities were surveyed in five habitats (tidal forest, oak forest, pine forest, shrub and saltmarsh) of coastal Georgia, USA, using distance-sampling methods. Canonical Correspondence Analysis and Indicator Species Analysis showed that species associated with saltmarsh (e.g. Clapper Rail (*Rallus longirostris*)) and tidal forest habitats (e.g. Prothonotary Warbler (*Protonotaria citrea*)) were distinctively different than species associated with oak forest, pine and shrub habitats. Common Ground-Dove (*Columbina passerina*), Painted Bunting (*Passerina ciris*), Yellow-breasted Chat (*Icteria virens*) and Eastern Towhee (*Pipilo erythrophthalmus*) populations were associated with early-successional pine forest and shrub habitats, whereas Acadian Flycatchers (*Empidonax virescens*), Northern Parula (*Parula americana*), Yellow-throated Vireos (*Vireo flavifrons*), Yellow-throated Warblers (*Dendroica dominica*), Summer Tanagers (*Piranga rubra*) and Eastern Wood-Pewees (*Contopus virens*) were associated with mature pine, oak and tidal forests. Avian conservation practices in coastal Georgia should maintain and restore oak forest and shrub habitats, due to their limited area, while rotating pine forest in optimal conditions specific to target species. Distance-sampling methods should be used sparingly to assess species-habitat relationships, except when comparing among studies.

Keywords: avian, bird, conservation, population density, distance-sampling, indicator species analysis, canonical correspondence analysis, Georgia, habitat.

INTRODUCTION

Avifauna provide important ecosystem services, such as seed dispersal, pollination and insect control, but populations of most migrant birds have declined in recent decades (Kirk et al. 1996, Price and Root 2001, Rosenstock et al. 2002). There are currently 99 species of birds on the Partners In Flight (PIF) Watch List for North America out of the ~914 species found on the continent. Many others are priority species at the physiographic region scale (http://www.pwrc.usgs.gov/pif/WatchListNeeds/default.htm). The distribution of birds across a landscape ultimately depends on many factors, including habitat, available food, competition, climate, and physiology (Price and Root 2001), but maintaining viable avian populations requires accurate population parameter estimates, such as density and size (Buckland et al. 2001).

One of the principal methods used to determine abundance in avian conservation has been count data (Hodges and Krementz 1996, Bajema et al. 2001, Rosenstock et al. 2002). The point count method is relatively simple to conduct but assumes that bird detectability remains constant across different observer abilities, weather conditions, and species characteristics (Rosenstock et al. 2002), which is rarely the case in the field (Pacifici et al. 2008). Distance-sampling methods, as outlined by Buckland and others (2001), yield more precise estimates of bird density than index methods (e.g. point counts) by adjusting for detectability (Rosenstock et al. 2002, Thompson 2002). A seven-year comparison of point count methods versus distance-sampling found that the latter method was more robust in large-scale, multispecies surveys (Norvell et al. 2003).

Distance-sampling methods have been used in many studies to assess quantitative differences in habitat use by avian species as a way to distinguish species habitat preferences (Hodges and Krementz 1996, Estades and Temple 1999, Fletcher and Koford 2002). However, distance-sampling methods do not work well with rare species (Buckland et al. 2001). A relatively new method of assessing species-habitat relationships, indicator species analysis (ISA), is based on combining frequency of occurrence and mean abundance as developed by Dúfrêne and Legendre (1997), which is gaining use in conservation studies (Graham and Blake 2001, Kirk and Hobson 2001, Morissette et al. 2002, Mouillot et al. 2002, Grundel and Pavlovic 2007). ISA has the advantage of assessing species-habitat correlations when species are rare, non-normality exists, where distance-sampling may be logistically difficult, and where there are many cases of no detection of a species at sample sites by combining information on abundance and frequency of occurrence (Mouillot et al. 2002).

The south Atlantic coastal plain physiographic area covers about 25 million acres in parts of six states from Virginia to Alabama, has over 160 breeding bird species, contains the largest forested floodplains outside the Mississippi Alluvial Plain in North America, and has the "best remaining examples of 'natural' barrier and sea islands and maritime forests in the southeast" (Hunter et al. 2001). However, 40% of natural vegetation has been lost due to land conversion.

PIF prioritizes the conservation status of avian species based on six factors: population size, breeding distribution, non-breeding distribution, threats to breeding, threats to non-breeding and population trends, with scores for each factor ranging from low vulnerability (1) to high vulnerability (5) (Carter et al. 2000). The combined score for each species is determined by adding the scores of the population size and population trend factors with the highest of either the breeding or non-breeding density scores and the highest of either the breeding or non-breeding threat scores. The resulting total conservation status scores range from four (low priority) to 20 (high priority).

Within the south Atlantic coastal plain, PIF recognizes 14 distinct bird-habitat associations, including: 1) early successional shrub-scrub maintained by frequent and large-scale disturbance regimes, such as fire, 2) southern pine dominated by loblolly (*Pinus taeda*), slash

(*Pinus elliottii*) and longleaf pine (*Pinus palustris*) stands with frequent fires, 3) forested wetlands dominated by bald cypress (*Taxodium distichum*) and water tupelo (*Nyssa aquatica*), 4) maritime woodlands dominated by live oak (*Quercus virginiana*), and 5) estuarine emergent wetlands such saltmarsh (Hunter et al. 2001). Two additional PIF forest avian communities of interest not associated with any specific forest type include conifer-hardwood generalists and colonial tree nesting waterbirds (Hunter et al. 2001). The only extremely high priority species in the region is the Painted Bunting (avian scientific names and PIF priority status are given in Table 1). Other high priority species include Brown-headed Nuthatch, Northern Parula, Hooded Warbler, Yellow-throated Warbler, Seaside Sparrow, and Clapper Rail (Hunter et al. 2001). While prioritizing wildlife conservation habitats requires knowledge of the relative conservation importance of the above species, it should also account for parameters such as species richness, population densities within each habitat and the relative rarity of the habitat (New 1997, Balcombe et al. 2005).

The objective of this study was to use distance-sampling methods to determine the densities of breeding bird species, and avian-habitat relationships in five habitats of coastal Georgia (tidal-freshwater broadleaf deciduous forest, saltmarsh, maritime scrub-shrub, maritime broadleaf evergreen forest and maritime narrowleaf evergreen forest) using Indicator Species Analysis (ISA). Habitat characteristics were correlated for each species using Canonical Correspondence Analysis to evaluate avian habitat management needs. We also compared distance-sampling and ISA methods of assessing species-habitat relationships to determine methodological biases in characterizing avian communities.

METHODS

Study Area

Five habitats (tidal-freshwater broadleaf deciduous forest, saltmarsh, maritime scrub-shrub, maritime broadleaf evergreen forest, and maritime narrowleaf evergreen forest) in coastal Georgia, USA, were surveyed for breeding birds (Fig. 1). The tidal fresh-water broadleaf deciduous forest (tidal forest) was located in the Clayhole Swamp Wildlife Management Area on the south side of the Altamaha River in Glynn County, and is managed by the Georgia Department of Natural Resources. The other four habitats were on the 6,677 hectare (hectare = 10,000 m^2) Sapelo Island, McIntosh County, on property owned by the Georgia Department of Natural Resources (GNDR) and the Sapelo Island National Estuarine Research Reserve, and managed by GDNR. Sapelo Island saltmarsh habitat (saltmarsh) was located on the southwestern portions of the island. Maritime scrub-shrub habitat (shrub) was located primarily in linear landscape features, such as secondary dunes and on the edge between forest and saltmarsh. Maritime broadleaf evergreen forests (oak forest) were dominated by live oak, and located primarily on the north end of the island. Maritime narrowleaf evergreen forests (pine forest) were dominated by loblolly pine with scattered slash pine and were evenly distributed throughout the island. While Sapelo Island pine forests were not plantation plantings, they were regularly managed by fire and timber harvest.

All bird sample points were located at least 250 m apart. In the tidal forest, they were distributed on a grid starting from the southernmost accessible point via Honeygal Road. On Sapelo Island, saltmarsh sample points were distributed based on the random selection of 1-m^2 grids within the marsh, overlain on a GIS shapefile, using a random number generator. In the linear shrub habitat, sample points were located in the middle of the scrub-shrub ecotone between primary dunes and terrestrial forests on Sapelo Island. Oak and pine forest sample points were located by driving on dirt paths through forested sections, identifying the dominant forest type in a patch (pine or oak) and randomly locating the point between 10 and 200 m on a line perpendicular to the dirt path.

Bird Sampling

Point counts generally followed the methods established by Ralph et al. (1993). Ten points were located in each habitat in 2006. An additional 20 points per habitat were established in 2007 (30 points in each habitat). Ten-minute point counts were conducted twice, at least two weeks apart, at each point within 4 hr of sunrise between 19 May and 9 June 2006, and between 17 May and 13 June 2007, for a total of 100 sampling events in 2006 and 300 sampling events in 2007. During each sampling event, the relative direction and distance of each detected bird was estimated within 5 m intervals from the sample point, except for flyovers, by the same person. Distance estimations were verified in the field on the way to the next point by stepping off the distance from the point just sampled to a detected bird and adjusting the distances as necessary. Detections of the same species only included birds detected simultaneously or with obvious differences in plumage. While distance-sampling and ISA included all species detected, species of interest for discussion were limited to PIF species of concern listed for early successional shrub-scrub, southern pine, forested wetlands, maritime woodlands, emergent wetlands, colonial tree-nesting waterbirds and conifer-hardwood generalists (Hunter et al. 2001).

Population Densities

The density (# of birds/ha) of species sampled using point counts was estimated in the program *Distance 5.0* (Thomas et al. 2006) by the equation:

$$D = n / kv$$

Where D = density of birds per unit area, n = number of birds detected, k = the number of points sampled, and v = the detection function of the species with distance from the sample point. Each species has a detection probability function that indicates probability of detection as a function of distance from the sample points (Buckland et al. 2001). *Distance* calculates detection functions from the center point to individual birds based on fitting the empirical data to four potential probability density functions. The four theoretical models of probability density functions are: the uniform distribution, the half-normal distribution, the hazard-rate distribution and the negative exponential distribution, each of which can go through three series expansions (cosine, simple polynomial and hermite polynomial) for a total of 12 potential models. The density of each species is calculated by fitting the frequency of detection as a function of distance into each of the 12 theoretical models and determining the best fitting model: the one with the lowest Akaike's Information Criterion (AIC) value (Buckland et al. 2001). The frequency distribution of distance to detected birds for each species was pooled across all habitats to increase the sample size of the detection functions.

Buckland and others (1993) note that 70-100 detections are generally required to estimate accurate densities. For rare species, *Distance* allows the use of proxy detection functions of other species that have similar detectability (Buckland et al. 1993, Grundel and Pavlovich 2007). Proxy species were used for 22 of 49 species (Table 1) and grouped by similarities in lifestyle, size and detectability, such as herons and egrets. The cutoff for exclusion from *Distance* analysis was less than two individuals of a species in a given habitat or less than five observations for a species across all habitats. Fourteen species [Black Vulture (*Coragyps atratus*), Cooper's Hawk (*Accipiter cooperii*), Great-horned Owl (*Bubo virginianus*), Eurasian-collared Dove (*Streptopelia decaocto*), Gray Catbird (*Dumetella carolinensis*), Hairy Woodpecker (*Picoides villosus*), Indigo Bunting (*Passerina cyanea*), Louisiana Waterthrush (*Seiurus motacilla*), Osprey (*Pandion haliaetus*), Plain Chachalaca (introduced, *Ortalis vetula*), Snowy Egret (*Egretta thula*), Tri-colored Heron (*Egretta tricolor*), Wood Stork (*Mycteria americana*), and Wood Thrush (*Hylocichla mustelina*)] were considered so rare that they were not included in the analysis.

Species were considered to be associated with a habitat using *Distance* analysis by being detected only in that habitat on at least five occasions, or by a lack of overlap of the 95% confidence intervals between habitat types (Hodges and Krementz 1996, Fletcher and Koford 2002).

Distance requires detection functions to monotonically decrease with distance from the sample point such that the detection function is either flat or decreases with distance (Thomas et al. 2006). If the detection function increases with distance, then *Distance* will constrain the parameters of the detection function at fixed points in order to fit the function to the model. However, these constraints obviously distort the detection function which may be better adjusted by truncating the tail of the data, altering the intervals, or using proxy species to smooth the detection function (Thomas et al. 2006). In order to prevent the parameters from being constrained to obtain monotonicity, White-eyed Vireo models were run by combining the 5 m intervals detected in the field into 10 m intervals in *Distance*.

Habitat Characteristics

Percent total forest cover, broadleaf forest cover, narrowleaf forest cover, subcanopy cover, sapling/shrub cover, dead shrub cover, herbaceous cover and litter cover were visually estimated with a Geographic Resource Solutions (Arcata, California) densitometer for each sample point. Broadleaf forest, narrowleaf forest, subcanopy, and sapling/shrub heights (in m) were measured at each sample point using a clinometer, herbaceous height (in cm) was measured with a measuring stick. Stem densities of trees and saplings/shrubs (number of stems/m^2) were calculated from the number of stems within 10 m of each sample point. The diameter at breast height (dbh) for each tree within 10 m of each sample point was measured, the cross-sectional area of each tree was calculated from the dbh, and the basal area of tree species for the sample point were calculated by summing the cross-sectional area of each tree species at the sample point. In saltmarsh, the stem density of *Spartina alterniflora* was measured by counting the number of stems within a 0.5 m^2 plot, and the height of the tallest stem also was measured (in cm).

Using a Geographical Information System (GIS) dataset of coastal Georgia from the National Wetland Inventory (available at: http://www.fws.gov/data/statdata/GAdata.html) and a GIS dataset of land cover on Sapelo Island from the Georgia Department of Natural Resources in ArcMap 9.2 (Environmental Systems Research Institute, Redland, California), the distance to the nearest transition to another habitat, water source and patch of similar habitat greater than 40 hectares was measured for each sample point. In saltmarsh habitat, the nearest edge of interest was any terrestrial patch. In oak forest, the nearest edge of interest was pine forest, and vice versa. The tidal forest edge of interest was the nearest road, and shrub habitat edge was the nearest saltmarsh. The patch area of each habitat sample site was also calculated in ArcMap 9.2.

Statistics

Species-habitat associations were assessed using Indicator Species Analysis (ISA; McCune and Grace 2002). ISA first calculates the mean proportion of abundance of a species within a group (e.g. habitat type) taken from the point count totals for each site, then the proportion of sample units (e.g. sites) in each group that contain a species, and multiplies the proportions together to create an indicator value of the species in each group. The highest observed indicator value for a given species is compared to indicator values generated by randomly reassigning sample units among groups using Monte Carlo methods to test the null hypothesis that the highest indicator value is no greater than expected by chance (McCune and Grace 2002). ISA was conducted in PC-ORD (McCune and Mefford 2006) using 9999 Monte Carlo iterations. Reported ISA results include the relative abundance, relative frequency, highest indicator value, and the *P*-values of significant differences. (Throughout this paper, statistical results were considered significant at $\alpha < 0.05$.) Dúfrêne and Legendre (1997) recommend a cutoff threshold indicator value (IV) of 25 for a species to be considered truly indicative of a habitat. ISA analysis here presents the results with and without using the IV > 25 cutoff.

Canonical Correspondence Analysis (CCA) was conducted to analyze the relationship between community structure of avian species of concern and habitat characteristics in PC-ORD (McCune and Mefford 2006). Due to changes in habitat structure from fire, flood and wind disturbance, each site was treated separately each year (50 in 2006 and 150 in 2007 for a total of 200 sites). Of the original 24 habitat characteristics, 12 variables were eliminated from the analyses by removing highly correlated ($r > \pm 0.7$) habitat characteristics, and then a backward selection procedure was used to determine the smallest subset that best described the relationships. In the final analyses, six habitat characteristics were used: % forest cover, basal area of tupelo gum trees, basal area of other tree species, sapling height, % herbaceous cover, and % litter cover. CCA scores were standardized by centering and normalizing, and the ordination scores were scaled by optimizing the sites (rows). The null hypothesis of no relationship between matrices was tested in PC-ORD using 9999 Monte Carlo iterations.

RESULTS

Raw Detections

Overall, there were 73 species detected during the two breeding seasons. Northern Cardinals and Carolina Wrens were detected most often (401 and 400 across the five habitats, respectively). Within each habitat, Red-eyed Vireos were most abundant in tidal forest (142), Northern Parula in oak forest (180), Red-bellied Woodpecker in pine forest (116), Clapper Rail in saltmarsh (150), and Northern Cardinal in shrub (140). The number of detections per species in each habitat are given in Table 1.

Distance-sampling bird densities

Overall, breeding bird densities were estimated for 48 species in *Distance* (Table 2). In tidal forest, densities of 24 species were estimated. Four species (Prothonotary Warbler, Red-shouldered Hawk, Yellow-billed Cuckoo and Yellow-crowned Night Heron) were unique to tidal forest and Red-eyed Vireo populations were significantly more dense in tidal forest than other habitats. Blue-gray Gnatcatchers were the most dense species in tidal forest (2.35 birds/ha).

Density of breeding birds in saltmarsh habitat was estimated for 12 species, ten of which (Clapper Rail, Eastern Kingbird, Great Blue Heron, Great Egret, Green Heron, Marsh Wren, Seaside Sparrow, Willet and Wilson's Plover) were unique to saltmarsh (Table 2). Red-winged Blackbirds had the highest density in saltmarsh (1.25 birds/ha).

In shrub habitat, densities of 30 species were estimated, and two (Northern Mockingbird and Orchard Oriole) were unique to this habitat (Table 2). Both Eastern Towhee and Painted Bunting populations were more dense in shrub than other habitats. The highest mean estimated breeding bird density in shrub habitat was for Blue-gray Gnatcatcher (5.32 birds/ha).

Thirty-one species' densities were estimated in oak forest using *Distance*, none of which was unique to this habitat (Table 2). Northern Parula was the only species that had significantly higher density in oak forest than other habitats. Blue-gray Gnatcatchers had the highest mean density in oak forest (5.72 birds/ha).

Breeding bird densities were estimated for 34 species in pine forest, but none was unique to this habitat (Table 2). Both Brown-headed Nuthatch and Pine Warbler had significantly higher estimated mean densities in pine forest than other habitats. The highest mean density in pine forest was for Brown-headed Nuthatch (5.96 birds/ha).

Indicator Species Analysis

Forty-eight species were indicative of one of the five habitats in coastal Georgia (Figure 2). Eleven species were indicative of tidal forest, only six of which were above Dúfrêne and Legendre's (1997) IV > 25 cutoff, and five were PIF priority species. Eleven species were indicative of saltmarsh, but only five were above the cutoff IV and three were PIF priority species. Shrub habitat had only eight indicator species, four above the cutoff IV and five PIF priority species, including Painted Bunting, the only extremely high priority species in the region. Nine species were also indicative of oak forest, but Carolina Chickadees were below the cutoff (IV = 20.5) and five were PIF priority species. Nine species were also indicative of pine forest, five of which were above the cutoff IV score, and three were PIF priority species. The oak forest and shrub habitat species with the highest IV scores (Yellow-throated Warbler and Painted Bunting, respectively) had lower IV scores than the species with the highest IV scores in pine forest, saltmarsh and tidal forest (Brown-headed Nuthatch, Clapper Rail and Red-eyed Vireo, respectively).

Sample point vegetation characteristics

Tidal forest sites had the highest forest cover, broadleaf cover, broadleaf height and tree stem density (Table 3). Saltmarsh sample sites were the closest to edges, roads, water and patches > 40 ha, and had the highest herbaceous cover and lowest litter cover. Sapling cover, dead sapling cover, sapling height, herbaceous height and sapling stem density were highest in shrub habitat. Oak forest sites were the farthest from paved roads, had the lowest herbaceous cover and herbaceous height, and the highest litter cover and live oak basal area. Pine forest sites were farthest from edges, water and patches of similar habitat > 40 ha, and had the highest narrowleaf cover, narrowleaf height, subcanopy cover, pine tree basal area and subcanopy height.

Canonical Correspondence Analysis

Axis 1 and Axis 2 of the CCA were significantly correlated between habitat and species with eigenvalues of 0.623 and 0.353, respectively (P = 0.0001). Axis 1 explained 13.5% of the variance in the species data and Axis 2 explained 7.7%. Axis 1 was negatively correlated with percent litter cover (r = 0.872), forest cover (r = -0.669) and sapling height (r = -0.566), but positively correlated with percent herbaceous cover (r = 0.401). Axis 2 was positively correlated with basal area of tupelo gum trees (r = 0.680), percent forest cover (r = 0.601) and basal area of other tree species (r = 0.558). Pearson correlations between species ordination scores and environmental variable scores (species-environment correlations) were 0.815 for Axis 1 and 0.842 for Axis 2 (P = 0.0001).

A biplot of CCA results showed that Axis 1, most related to litter and forest cover, separated the saltmarsh sites and species from the terrestrial/forest sites and species (Fig. 3a and 3b). Axis 2, most related to basal area, separated the tidal forest sites and species from the other habitats. The remaining shrub, oak and pine forest habitats were clustered together in the middle of the biplot, but each habitat occupied a different region of the graph (Figure 3a). Three species (Hooded Warbler, Prothonotary Warbler and Yellow-billed Cuckoo) were associated with tidal forests that had high basal areas of tidal forest tree species, whereas Yellow-crowned Night Heron and Acadian Flycatcher were associated with regions of lower basal areas tidal forest tree species. Acadian Flycatchers were also associated with dense forest canopy cover. Clapper Rails, Great Egrets and Seaside Sparrows were associated with saltmarsh sites that had more herbaceous cover, while Great Blue Herons were associated with saltmarsh sites with less herbaceous cover (Figure 3b). Five species (Common Ground-Dove, Eastern Towhee, Orchard Oriole, Painted Bunting and Yellow-breasted Chat) were associated with more developed shrub habitats with higher herbaceous cover and sapling heights. Northern Parula and Summer Tanagers were associated with mature forest patches with high forest and litter cover, but low sapling heights, typical of mature live oak forest and tidal forests. Brown-headed Nuthatches, Pine Warblers, and Red-headed Woodpeckers were associated with thinly forested pine sites with high litter cover and sapling heights typical of early-successional pine forests. Eastern Wood-Pewees, Yellow-throated Vireos and Yellow-throated Warblers occupied sites with intermediate levels of forest cover and high sapling height typical of mid-successional terrestrial forests.

Discussion

Distance-sampling bird densities

Distance-sampling has generally been used less frequently than conventional point count methods due to the perception that it is difficult, expensive and time-consuming, but a direct comparison of the methods showed that distance-sampling was more reliable despite these difficulties (Norvell et al. 2003). Assumptions in distance-sampling include complete detection of all individuals close to the sample point and that birds do not leave the sampling area prior to detection (Buckland et al. 1993, Thompson 2002). In this study, the detection rates generally increased within the first 5-10 meters of the sample point before beginning to descend, indicating that birds may have moved from the sample point as the observer approached, or that the area of near perfect detection extended ~5 m beyond the sample point itself. However, using 5 m intervals should have offset any potential movement, allowing *Distance* to successfully model the densities. We were also unable to create an acceptable detection function for White-eyed Vireos without increasing the interval width from 5 m to 10m, indicating a potentially greater response to the observer approach or wider area of near perfect detection for this species.

Acceptable detection functions were unable to be calculated for four species (Great Blue Heron, Great Egret, Snowy Egret and Yellow-crowned Night Heron), even with proxies, However, the four species were all from the heron family (*Ardeidae*), which should have near complete detection due to their conspicuous size and sounds.

Buckland et al. (1993) note that 70-100 detections are generally required to estimate accurate densities. Twenty-two of our 49 species required the use of proxies to generate enough samples for acceptable detection functions in *Distance*. Proxy species were grouped by similar lifestyle, size and detectability to reduce the effects of the added species. Due to the use of proxies, density estimates for these locally rare species should be viewed with some caution.

Forest structure is expected to skew detection of silent and sedentary individuals, whereas more open habitats, such as saltmarsh, should allow for near complete detection (Pacifici et al. 2008). Thus, breeding bird density estimates in forested habitats were likely underestimated. Simons et al. (2007) particularly emphasize the need to account for detection variations among different habitats, limiting the pooling of data to create the detection functions. However, we felt the need for increased sample size in creating the detection function outweighed the differences between habitats. The observer considered the species detectability in the three forest habitats to be equally altered by vegetation structure, and the saltmarsh was so different in species composition and open vegetation structure that standard distance-sampling methods would account for this habitat. However, shrub habitat had less vegetation structure than the forests to impede species detection, but more wind disturbance than the forest habitats, potentially offsetting the effects.

Some of the population densities appear high, particularly Blue-gray Gnatcatchers in all habitats except saltmarsh, Brown-headed Nuthatches in pine forest, Northern Parula in oak forest and White-eyed Vireos on Sapelo Island. Brown-headed Nuthatches, found almost exclusively in pine forests, were observed traveling in family groups that may have skewed results by including more young-of-year than other species. On the other hand, Northern Parula detections were comprised of mostly singing males, which were definitively more abundant in oak forest. White-eyed Vireos and Blue-gray Gnatcatchers seemed curious about my presence at the sample point, which may have positively skewed their results.

Comparisons of bird densities in this study to riparian corridors of different widths up to 186 km further upstream of the Clayhole Swamp on the Altamaha River are possible for Acadian Flycatcher, Blue-gray Gnatcatcher, Northern Parula, Prothonotary Warbler, Red-eyed Vireo and White-eyed Vireo (Hodges and Krementz 1996). Estimated densities measured by Hodges and Krementz (1996) upriver of the Clayhole Swamp were generally lower than found in coastal habitats in this study for all six species. However, these differences may be due to variations in study design or individual bird detection skills. Northern Parula densities in upstream riparian corridors were similar to shrub habitat (Hodges and Krementz 1996).

Comparison of distance-sampling and Indicator Species Analysis

Overall, distance-sampling methods listed less than half of the species having significantly higher densities than ISA (Figure 2). However, using the IV > 25 cutoff recommended by Dúfrêne and Legendre (1997), the results were more comparable in number (28 vs. 22), but not necessarily in composition. In tidal forest habitat, ISA identified Acadian Flycatcher as an indicator species, a PIF priority species of local interest (Hunter et al. 2001), whereas distance-sampling methods replaced Acadian Flycatcher with Red-shouldered Hawk and Barred Owl. Distance-sampling analysis in saltmarsh included Seaside Sparrow (PIF high priority), Willet (PIF moderate priority) and Wilson's Plover (PIF high priority) that were all excluded by ISA using the IV > 25 cutoff, but ISA included Boat-tailed Grackle that was missed by distance-sampling. In shrub habitat, Yellow-breasted Chat and Northern Cardinal were listed as indicator species by ISA and not distance-sampling, but Common Ground-Dove (PIF moderate priority), Northern Mockingbird and Orchard Oriole (PIF moderate priority) were listed as indicator species by distance-sampling and not ISA. However, the greatest differences occurred in oak forest with seven species that ISA considered indicators that distance-sampling techniques excluded (Blue-gray Gnatcatcher, Carolina Wren, Eastern Wood-Pewee, Great-crested Flycatcher, White-eyed Vireo, Yellow-throated Vireo and Yellow-throated Warbler). Four of the ISA species excluded by distance-sampling in oak forest were also listed as PIF priority species for the region (Eastern Wood-Pewee, White-eyed Vireo, Yellow-throated Vireo and Yellow-throated Warbler). Both Red-bellied Woodpecker and Red-headed Woodpecker, a moderate PIF priority species, were indicative of pine forest using ISA, but were excluded by distance-sampling methods.

Distance-sampling underestimated the number of species associated with certain habitats by more than 50% compared to ISA if no cutoff is used . The main reasons for the lack of species-habitat associations in distance-sampling are that the analysis is conservative by definition (no overlap of 95% confidence intervals) and excludes rare species that ISA analyzes. Distance-sampling methods specifically excluded eight PIF priority species that are in need of conservation management, indicating that using this method to assess habitat associations may cause important or rare species to be left out of planning strategies. ISA was clearly the best method at classifying a broad range of species with their associated habitats regardless of rarity within the region. However, ISA measures are specific to the habitats sampled in the study and cannot be compared among habitats in other studies, whereas breeding bird density estimates from distance-sampling can be compared across different habitats. Using the IV > 25 cutoff created similar numbers of indicator species using both ISA and distance-sampling, but distance analysis still lacked the rare species and ISA included several "borderline" species that use several habitats (e.g., Acadian Flycatcher, Northern Cardinal and Blue-gray Gnatcatcher).

Canonical Correspondence Analysis

Researchers have used CCA for assessing avian response to landscape characteristics using GIS landscape variables alone (Coppedge et al. 2001, Miller et al. 2004) or in combination with local habitat measurements (Bolger et al. 1997, Hennings and Edge 2003, Melles et al. 2003, Miller et al. 2003). However, GIS variables were not significant in this CCA analysis. The lack of correlation between GIS landscape variables and avian communities was likely due to the fact that tidal forest and pine forest sampling points were located primarily within the same large patches, and the birds may have adapted to the naturally patchy landscape of coastal Georgia. In particular, the species most associated with shrub habitat were also found in terrestrial forested habitats. Since landscape-scale spatial measurements had little correlation with avian species distributions, birds of coastal Georgia appear to be distributed based on local habitat characteristics, competition and food availability rather than larger-scale landscape features.

The forest and shrub birds of coastal Georgia were distributed mostly by the upper strata structure and its effect on the lower strata. For example, oak forest and tidal forest canopies were closed, limiting the development of their herbaceous and sapling layers compared to those layers in pine forest and shrub. However, pine forest was modified by management activities such that more recently harvested or burned pine stands had higher sapling and herbaceous cover, whereas older, unburned pine stands had more developed subcanopies and less herbaceous cover (pers. obs). Shrub-related avian species (such as Yellow-breasted Chat and Painted Bunting) can use maritime shrub, or early-successional pine forest recovering from logging and burning activities, but appear to prefer one habitat over the other. For example, Painted Buntings prefer shrub habitat, whereas Yellow-breasted Chat appear to prefer early successional pine forest.

Avian communities in tidal and terrestrial forests were generally those observed by Hamel (1992), with notable exceptions due to differences in localized habitat preferences. For example, Wood Thrush were not abundant in any of these forests, presumably due to lack of litter in tidal forest and pine forest and lack of herbaceous cover in oak forest. Yellow-throated Warblers and Red-headed Woodpeckers were likely absent from tidal forest from lack of open canopy or big dead trees, respectively. In oak forest, Yellow-breasted Chat, Seaside Sparrow, Orchard Oriole, Common Ground-Dove and Clapper Rail were probably absent due to the dense forest canopy cover limiting herbaceous and shrub development. Hooded Warbler and Common Ground-Dove were both absent from pine forest despite Hamel's expectations, possibly due to lack of midstory development and bare soil, respectively.

Implications for Conservation

Tidal forest, which occupies ~10.0% of the coastal Georgia landscape (Brittain et al. 2009), contributed a disproportionate number of unique priority species. As with other studies, Prothonotary Warblers were found in tidal forest sites with high forest cover and basal area along tidal channels (Petit 1999). However, the patch size of the Clayhole Swamp (1221 ha) is only half that considered necessary to be a source patch (Hunter et al. 2001). Similarly, Acadian Flycatchers and Yellow-billed Cuckoos were indicative of wetland forests typical of their southeastern habitats (Stevenson and Anderson 1994, Whitehead and Taylor 2002), although Acadian Flycatchers were also abundant in oak forest. Hooded Warblers occupied sites in mature moist forests with lower sapling cover than found in other studies (Ogden and Stutchbury 1994). Typical of their broad forest associations, Carolina Chickadees were abundant in all three forest types, with no habitat preference. Yellow-throated Warblers were not found in tidal forests, despite another study that observed them there (Hall 1996), and may have also been deterred from occupying tidal forests by a lack of large dead trees (Hamel 1992). Tidal forest of the Clayhole Swamp noticeably lacked Mississippi Kites (*Ictinia mississippiensis*), Cerulean Warblers (*Dendroica cerulea*) and Swainson's Warblers (*Limnothlypis swainsonii*), which are priority species for floodplain forested wetlands (Hunter et al. 2001). Forest density and thick canopy cover in the tidal forest may have also prevented species expected in oak-gum-cypress forests of the southeast from occupying this habitat, such as Great Blue Heron, Great Egret, Snowy Egret, Marsh Wren, Painted Bunting, Red-headed Woodpecker and Yellow-breasted Chat (Hamel 1992). Louisiana Waterthrush was rarely detected in the tidal forest, as expected, but this habitat should have been optimal for Wood Thrush (Hamel 1992).

Georgia saltmarshes had the lowest diversity of priority species, but all four species were unique to this habitat. Seaside Sparrows were found exclusively in tall *Spartina* stands along larger estuaries where they have ample foraging mudflats available (Post and Greenlaw 1994). Clapper Rails were not as specific to tall *Spartina* saltmarsh as Seaside Sparrows since they were more evenly detected across the saltmarsh landscape, likely due to an ability to use the shrubby vegetation in high marsh regions (Eddleman and Conway 1998). Zones of tall *Spartina* along tidal channels may be important to provide habitat for Seaside Sparrows and other saltmarsh birds, such as Marsh Wrens (*Cistothorus palustris*), by creating areas of dense vegetation for secure nests.

In coastal Georgia, Eastern Towhees and Yellow-breasted Chats were far more abundant in shrub habitat than in open forest habitats also commonly associated with these species (Greenlaw 1996, Eckerle and Thompson 2001). Similarly, Common Ground-Doves and Orchard Orioles were found only in coastal dunes despite known additional use of open pine, hammocks and forest edges common on Sapelo Island (Scharf and Kren 1996, Bowman 2002). The PIF Conservation Plan defines quality shrub habitat as “largely forested areas with some edge and forest openings for buntings” (Hunter et al. 2001). However, shrub habitat where Painted Buntings, Eastern Towhees and Yellow-breasted Chats were far more abundant in this and another study (Springborn and Meyers 2005) was largely composed of coastal dunes. Prime maritime scrub-shrub habitat deserves conservation priority since it occupied such a small proportion of the coastal Georgia landscape (~0.2%; Brittain et al. 2009).

Oak forest had 14 PIF priority species, many of which were conifer-hardwood generalists, but White-eyed Vireos and Eastern Towhees were priority species for shrub habitats rather than oak forest. ISA showed White-eyed Vireos were actually indicative of oak forest and Eastern Towhees of shrub habitat. Northern Parula occupied mature hardwood forests with Spanish moss (oak forest) and floodplains with blue palm (tidal forest) as seen by Moldenhauer and Regelski (1996), but were far more abundant in oak than floodplain forests. Similarly, Eastern Wood-Pewee and Yellow-throated Vireo were found in all three forest types, but were more common in oak forest sites with more subcanopy structure (McCarty 1996, Rodewald and James 1996). Yellow-throated Warbler populations were most dense in oak forest. Similar to the results of Springborn and Meyers (2005), Painted Buntings were particularly found in oak forest sites located within 300 m of a saltmarsh edge. However, another species of concern for maritime forest and early successional shrub, Common Ground-Dove, was never seen in this habitat during the two year study, likely due to the lack of bare soil (Hamel 1992). Five species associated with live oak maritime forest by Hamel (1992) were likely not detected in oak forest because of their associations with water, Great Blue Heron, Great Egret, Snowy Egret, Clapper Rail and Seaside Sparrow. Acadian Flycatcher, Yellow-throated Vireo, Brown-headed Nuthatch and Pine Warbler were not expected to be found in oak forest (Hamel 1992) but were actually common, likely due to the presence of scattered large pine trees in oak patches.

Species associated with pine forest were those expected to be found in southern pines. Pine Warblers and Red-headed Woodpeckers were most associated with mature stands of pine with well-developed shrub strata, but also found in mixed oak and pine forests, confirming other studies (Rodewald et al. 1999, Smith et al. 2000). Summer Tanagers were present in all three forest types, with no preference between them, despite previous studies showing a preference for mixed pine and oak forests (Robinson 1996). Brown-headed Nuthatches were found in more open, mature pine stands as seen by Withgott and Smith (1998). A PIF Conservation Plan goal in pine forest includes emphasis on late successional stands with increasing disturbance regimes in order to increase understory habitat quality (Hunter et al. 2001), and managed disturbances such as prescribed fire and logging on Sapelo Island maintain the open stands of mature pine habitat preferred by Brown-headed Nuthatches. However, while this conservation plan may aid Brown-headed Nuthatches and Red-headed Woodpeckers it may also harm Pine Warbler populations dependent on a well-developed shrub layer. Since pine forest occupied such a large proportion of the coastal Georgia landscape (~48.8%), there is opportunity for diverse strategies to protect species associated with this habitat. Great Blue Herons, Yellow-billed Cuckoos, Prairie Warblers and Orchard Orioles were not associated with loblolly-shortleaf pine according to Hamel (1992), but were detected in pine forest. Conversely, Common Ground-Doves, Hooded Warblers and Wood Thrushes were conspicuously absent from pine forest.

In conclusion, tidal forest had the most indicator species of the five habitats sampled in coastal Georgia (10). However, shrub habitat had the highest conservation importance since it tied tidal and oak forest for the most number of PIF indicator priority species (5), had the only extremely high priority indicator species (Painted Bunting), and occupied a much smaller portion of the coastal landscape (~0.2%). Oak forests, tidal forests and saltmarsh cover moderate proportions of the coastal Georgia region, but the forest habitats both had more PIF priority indicator species than saltmarsh. The protections given tidal wetlands under Section 404 of the Clean Water Act (e.g. tidal forest and saltmarsh; PL 92-500, 33 USC 1251), combined with the high percentage of priority species, implies that oak forest should have higher avian conservation importance than tidal forest and saltmarsh. Pine forest is relatively plentiful and had the least number of total indicator species and PIF priority indicator species of any habitat. Care should be taken to maintain and restore some of the oak forest and shrub habitats while rotating pine forest in optimal conditions specific to target species in avian conservation.

Avian community response to disturbances such as tropical storms, logging and burning would likely be increased numbers of Common Ground-Dove, Painted Bunting, Brown-headed Nuthatch, Red-headed Woodpecker, Yellow-breasted Chat and Eastern Towhee, because these populations are associated with early-successional pine forest and shrub. Concurrently, these disturbances would likely decrease Acadian Flycatcher, Northern Parula, Yellow-throated Vireo, Yellow-throated Warbler, Summer Tanager and Eastern Wood-Pewee populations, which occupy mature forests. Additionally, distance-sampling methods should be used sparingly to assess species-habitat relationships, except when comparing among studies.

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Table 1. Total detections (counts) and breeding bird population density (Birds/ha) with 95% confidence interval (in parentheses) for birds breeding in five habitat of coastal Georgia calculated using *Distance* software. Model definitions: un = uniform distribution, hn = half-normal distribution, hr = hazard rate distribution, ne = negative exponential distribution, cos = cosine series expansion, sp = simple polynomial series expansion, and hp = hermite polynomial series expansion. Proxies are the species used to create the distance detection function when the species being modeled had a small sample size. *††††* = extremely high priority species, *†††* = high priority species, *††* = moderate priority species, and *†* = local interest species (Hunter et al. 2001).

		Tidal forest	Oak forest	Pine forest	Saltmarsh	Shrub
Species	Model	Birds/ha	Birds/ha	Birds/ha	Birds/ha	Birds/ha
Great Blue Heron*[2]	counts	-	-	1	4	-
†Ardea herodias	un+sp	-	-	-	0.02 (0.00-0.06)	-
Great Egret*[2]	counts	-	-	-	14	-
†Ardea alba	un+sp	-	-	-	0.06 (0.02-0.12)	-
Snowy Egret*[2]	counts	-	-	-	2	-
†Egretta thula	-	-	-	-	-	-
Yellow-crowned Night Heron*[2]	counts	6	2	-	1	-
†Nyctanassa violacea	un+sp	0.02 (0.01-0.05)	-	-	-	-
Clapper Rail	counts				150	
†††Rallus longirostris	ne+sp	-	-	-	0.98 (0.58-1.63)	-

Red-shouldered Hawk[8]	counts	9	-	1	-	-
Buteo lineatus	ne+cos	0.04 (0.02-0.10)	-	-	-	-
Red-tailed Hawk[8]	counts	-	3	4	-	-
Buteo jamaicensis	ne+cos	-	0.02 (0.00-0.06)	0.02 (0.00-0.05)	-	-
Wilson's Plover[13]	counts	-	-	-	9	2
†††Charadrius wilsonia	hn+sp	-	-	-	0.08 (0.03-0.21)	-
Willet[13]	counts	-	-	-	9	2
††Tringa semipalmata	hn+sp	-	-	-	0.08 (0.03-0.21)	-
Mourning Dove	counts	2	7	26	-	9
Zenaida macroura	hn+sp	-	0.04 (0.02-0.10)	0.15 (0.07-0.31)	-	0.04 (0.02-0.09)
Common Ground-Dove*[5]	counts	-	-	-	-	5
††Columbina passerina	hr+sp	-	-	-	-	0.04 (0.02-0.10)
Yellow-billed Cuckoo	counts	30	1	1	-	1
††Coccyzus americanus	hn+sp	0.46 (0.25-0.84)	-	-	-	-
Barred Owl[8]	counts	5	-	-	-	-
Strix varia	ne+sp	0.02 (0.01-0.07)	-	-	-	-
Ruby-throated Hummingbird	counts	2	3	3	-	3
Archilochus colubris	hn+sp	0.21 (0.06-0.76)	0.31 (0.07-1.35)	0.31 (0.13-0.75)	-	0.31 (0.09-1.05)

Red-headed Woodpecker[9]	counts	-	6	19	-	2
††Melanerpes erythrocephalus	hr+sp	-	0.06 (0.03-0.14)	0.20 (0.11-0.35)	-	-
Red-bellied Woodpecker[12]	**counts**	**79**	**88**	**116**	**-**	**12**
Melanerpes carolinus	**hn+sp**	**0.69 (0.57-0.84)**	**0.80 (0.68-0.94)**	**1.00 (0.87-1.15) [b]**	**-**	**0.09 (0.04-0.21) [a]**
Downy Woodpecker	counts	18	27	23	-	14
Picoides pubescens	ne+hp	0.32 (0.14-0.73)	0.49 (0.22-1.07)	0.41 (0.18-0.95)	-	0.25 (0.11-0.60)
Pileated Woodpecker	counts	32	18	13	-	2
Dryocopus pileatus	ne+hp	0.22 (0.13-0.35)	0.12 (0.07-0.21)	0.09 (0.05-0.18)	-	-
Eastern Wood-pewee[7]	counts	1	37	41	-	-
†Contopus virens	hn+sp	-	0.40 (0.29-0.56)	0.44 (0.32-0.62)	-	-
Acadian Flycatcher	**counts**	**53**	**42**	**16**	**-**	**-**
†Empidonax virescens	**hn+sp**	**1.12 (0.83-1.52)**	**0.89 (0.62-1.27)**	**0.34 (0.19-0.59) [a]**	**-**	**-**
Eastern Kingbird[6]	counts	-	-	1	20	3
Tyrannus tyrannus	hn+sp	-	-	-	0.15 (0.09-0.27)	-
Great-crested Flycatcher[9]	**counts**	**26**	**78**	**63**	**-**	**19**
Myiarchus crinitus	**hr+sp**	**0.31 (0.22-0.43) [e]**	**0.90 (0.74-1.11)**	**0.73 (0.58-0.92)**	**-**	**0.20 (0.11-0.36) [e]**
White-eyed Vireo	**counts**	**17**	**140**	**101**	**-**	**99**
††Vireo griseus	**hn+sp**	**0.36 (0.19-0.66)[a]**	**2.85 (2.37-3.44)**	**2.08 (1.68-2.57)**	**-**	**1.97 (1.54-2.53)**

Yellow-throated Vireo	counts	2	33	22	-	1
†Vireo flavifrons	hn+sp	-	0.40 (0.25-0.65)	0.27 (0.15-0.48)	-	-
Red-eyed Vireo	**counts**	**142**	**19**	**10**	**-**	**1**
Vireo olivaceus	**ne+hp**	**1.77 (1.05-2.98)** [c]	**0.24 (0.12-0.48)**	**0.13 (0.06-0.29)**	**-**	**-**
Bluejay[4]	counts	12	10	18	-	3
Cyanocitta cristata	hr+sp	0.14 (0.06-0.31)	0.13 (0.08-0.22)	0.21 (0.12-0.38)	-	-
American Crow[1]	counts	7	10	13	-	4
Corvus brachyrhynchos	ne+sp	0.03 (0.01-0.09)	0.04 (0.01-0.13)	0.05 (0.02-0.16)	-	0.02 (0.00-0.07)
Fish Crow[8]	counts	-	16	8	-	4
Corvus ossifragus	ne+cos	-	0.06 (0.01-0.25)	0.03 (0.01-0.09)	0.03 (0.01-0.10)	0.02 (0.01-0.05)
Carolina Chickadee	counts	29	45	40	-	31
††Poecile carolinensis	hr+cos	0.79 (0.40-1.55)	1.20 (0.73-1.96)	1.04 (0.65-1.65)	-	0.74 (0.40-1.36)
Eastern Tufted Titmouse	**counts**	**86**	**70**	**52**	**-**	**6**
Baeolophus bicolor	**hn+sp**	**1.72 (1.38-2.14)**	**1.47 (1.14-1.88)**	**1.08 (0.78-1.51)**	**-**	**0.13 (0.05-0.33)** [a]
Brown-headed Nuthatch	**counts**	**-**	**11**	**114**	**-**	**9**
†††Sitta pusilla	**hn+sp**	**-**	**0.59 (0.34-1.00)**	**5.96 (4.70-7.55)** [c]	**-**	**0.48 (0.21-1.11)**
Carolina Wren	**counts**	**109**	**119**	**99**	**-**	**73**
Thryothorus ludovicianus	**hr+sp**	**0.94 (0.81-1.08)**	**1.03 (0.89-1.20)**	**0.88 (0.74-1.03)**	**-**	**0.64 (0.52-0.77)** [a]

Marsh Wren	counts	-	-	-	73	-
Cistothorus palustris	hn+sp	-	-	-	0.65 (0.34-1.26)	-
Blue-gray Gnatcatcher	**counts**	**23**	**56**	**55**	**-**	**53**
Polioptila caerulea	**hn+sp**	**2.35 (1.48-3.74)** [a]	**5.72 (4.40-7.45)**	**5.62 (4.34-7.28)**	**-**	**5.32 (3.86-7.32)**
Eastern Bluebird[3]	counts	-	-	13	-	-
Sialia sialis	hn+sp	-	-	0.19 (0.10-0.37)	-	-
Northern Mockingbird[4]	counts	-	-	2	-	5
Mimus polyglottos	hr+sp	-	-	-	-	0.06 (0.03-0.14)
Brown Thrasher[4]	counts	-	-	5	-	3
Toxostoma rufum	hr+sp	-	-	0.06 (0.02-0.16)	-	0.04 (0.02-0.09)
Northern Parula[11]	**counts**	**65**	**180**	**63**	**-**	**11**
†††Parula americana	**ne+cos**	**0.85 (0.60-1.21)**	**2.35 (1.74-3.16)** [c]	**0.81 (0.55-1.20)**	**-**	**0.09 (0.04-0.21)** [a]
Yellow-throated Warbler	**counts**	**-**	**139**	**91**	**-**	**19**
†††Dendroica dominica	**hr+cos**	**-**	**1.61 (1.30-1.99)**	**1.06 (0.83-1.34)**	**-**	**0.22 (0.12-0.42)** [a]
Pine Warbler	**counts**	**-**	**39**	**88**	**-**	**36**
††Dendroica pinus	**hn+sp**	**-**	**0.55 (0.38-0.79)**	**1.22 (0.95-1.56)** [c]	**-**	**0.48 (0.33-0.70)**
Prothonotary Warbler[10]	counts	23	-	-	-	-
††Protonotaria citrea	hn+sp	0.38 (0.22-0.68)	-	-	-	-

Common Yellowthroat[3]	**counts**	**-**	**4**	**19**	**-**	**5**
Geothlypis trichas	**hn+sp**	**-**	**0.04 (0.01-0.15)**	**0.20 (0.11-0.39) [d]**	**-**	**0.04 (0.02-0.10)**
Hooded Warbler	**counts**	**38**	**4**	**-**	**-**	**-**
†††Wilsonia citrina	**hn+sp**	**0.55 (0.32-0.94)**	**0.06 (0.02-0.21) [a]**	**-**	**-**	**-**
Yellow-breasted Chat	counts	-	-	10	-	34
†Icteria virens	hn+sp	-	-	0.15 (0.06-0.35)	-	0.49 (0.29-0.83)
Summer Tanager	counts	33	30	26	-	15
†Piranga rubra	hr+sp	0.35 (0.24-0.53)	0.35 (0.22-0.56)	0.30 (0.20-0.45)	-	0.17 (0.10-0.30)
Eastern Towhee	**counts**	**-**	**8**	**41**	**-**	**83**
††Pipilo erythrophthalmus	**hn+sp**	**-**	**0.11 (0.04-0.29) [a]**	**0.55 (0.38-0.80)**	**-**	**1.13 (0.87-1.48) [c]**
Seaside Sparrow[6]	counts	-	-	-	14	-
†††Ammodramus maritimus	hn+sp	-	-	-	0.13 (0.05-0.32)	-
Northern Cardinal	**counts**	**68**	**82**	**111**	**-**	**140**
Cardinalis cardinalis	**hr+sp**	**0.85 (0.66-1.09)**	**0.99 (0.81-1.19)**	**1.33 (1.12-1.59) [b]**	**-**	**1.70 (1.46-1.99) [f]**
Blue Grosbeak[3]	counts	-	-	6	-	12
Passerina caerulea	hn+sp	-	-	0.07 (0.02-0.20)	-	0.12 (0.06-0.25)
Painted Bunting	**counts**	**-**	**10**	**17**	**-**	**67**
††††Passerina ciris	**hn+sp**	**-**	**0.14 (0.07-0.27)**	**0.19 (0.10-0.37)**	**-**	**0.75 (0.53-1.05) [c]**

Red-winged Blackbird	**counts**	**-**	**-**	**-**	**148**	**37**
Agelaius phoeniceus	**ne+hp**	**-**	**-**	**-**	**1.25 (0.71-2.20) [c]**	**0.30 (0.15-0.58)**
Boat-tailed Grackle	counts	-	-	-	86	11
Quiscalus major	hn+sp	-	-	-	0.69 (0.43-1.09)	0.18 (0.05-0.61)
Brown-headed Cowbird	**counts**	**2**	**13**	**22**	**-**	**21**
Molothrus ater	**hn+sp**	**0.04 (0.01-0.19)**	**0.28 (0.14-0.55)**	**0.47 (0.28-0.80) [b]**	**-**	**0.26 (0.15-0.45)**
Orchard Oriole[3]	counts	-	1	2	-	13
††Icterus spurius	hn+sp	-	-	-	-	0.15 (0.07-0.32)

[1] Barred Owl as proxy detection function

[2] Great Blue Heron, Great Egret, Snowy Egret and Yellow-crowned Night Heron as proxy detection functions for each other

[3] Painted Bunting as proxy detection function

[4] Northern Cardinal as proxy detection function

[5] Eastern Towhee as proxy detection function

[6] Marsh Wren as proxy detection function

[7] Acadian Flycatcher as proxy detection function

[8] Barred Owl, Fish Crow, Red-tailed Hawk and Red-shouldered Hawk as proxy detection functions for each other

[9] Summer Tanager as proxy detection function

[10] Hooded Warbler as proxy detection function

[11] Pine Warbler as proxy detection function

[12] Downy Woodpecker as proxy detection function

[13] Ruddy Turnstone, Whimbrel, Willet and Wilson's Plover as proxy detection functions

[a] significantly lower than all other habitats

[b] significantly higher than tidal forest habitat only

[c] significantly higher than all other habitats

[d] significantly higher than shrub habitat only

[e] significantly lower than oak forest and pine forest habitats only

[f] significantly higher than oak forest and tidal forest only

Table 2. Habitat characteristics of five habitats in coastal Georgia. Measurements are in meters except where noted. Stem densities are in number of stems/m^2, herb height is in cm, and basal area is in cm^2. (n = 40 for each habitat type)

	Tidal forest	Oak forest	Pine forest	Saltmarsh	Shrub
	Mean (SD)	Mean (SD)	Mean (SD)	Mean (SD)	Mean (SD)
Distance to nearest edge	60.8 (50.1)	155.6 (68.2)	280.0 (241.9)	43.98 (35.78)	122.2 (81.2)
Distance to water	130.1 (116.1)	323.7 (225.5)	711.7 (385.5)	87.4 (135.1)	312.2 (337.5)
Patch area (m^2)	1221.2	382.9 (173.7)	1421.0 (761.0)	89.92 (54.8)	249.6 (551.8)
Distance to patch > 40 ha	2135.1 (384.6)	5563.0 (1969.0)	5894.0 (3948.0)	399.8 (273.6)	2980.0 (1435.0)
% forest cover	89.5 (7.67)	76.6 (12.0)	45.2 (15.1)	-	0.0
% broadleaf cover	70.3 (18.6)	66.2 (13.8)	3.0 (4.6)	-	1.8 (5.8)
% narrowleaf cover	19.0 (17.1)	10.5 (8.5)	42.2 (14.1)	-	6.2 (8.2)
Broadleaf tree height	28.9 (3.4)	25.4 (3.3)	11.8 (14.4)	-	1.8 (4.1)
Narrowleaf tree height	24.4 (11.7)	25.7 (.8)	29.5 (3.8)	-	6.0 (6.4)
Tree stem density	0.097 (0.038)	0.042 (0.020)	0.039 (0.028)	-	0.013 (0.016)
% subcanopy cover	14.2 (6.3)	20.8 (13.4)	20.8 (16.7)	-	8.8 (10.6)
Subcanopy height	10.3 (1.7)	10.8 (1.5)	12.0 (2.6)	-	7.2 (6.2)

% shrub/sapling cover	19.7 (14.8)	26.3 (21.6)	30.9 (23.4)	-	47.8 (16.4)
% dead shrub cover	-	-	-	-	4.6 (9.1)
Shrub/sapling height	2.8 (2.1)	2.6 (0.7)	2.7 (0.9)	-	4.0 (1.7)
Sapling stem density	0.225 (0.146)	0.134 (0.077)	0.191 (0.156)	-	0.358 (0.295)
% herbaceous cover	43.8 (28.9)	17.2 (14.9)	41.9 (31.2)	65.8 (18.5)	40.5 (24.2)
% litter cover	75.0 (25.4)	96.3 (3.6)	80.5 (18.8)	0.6 (1.7)	52.2 (27.3)
Herbaceous height	54.4 (14.6)	52.2 (23.7)	66.5 (45.5)	74.0 (23.0)	94.8 (27.1)
Herbaceous stem density	-	-	-	110.3 (28.2)	-
Basal area pine	0.0	208.6 (710.6)	2927.2 (2005.2)	-	172.2 (418.8)
Basal area live oak	0.0	5281.3 (4238.6)	248.9 (510.1)	-	158.2 (469.3)
Basal area tupelo gum	2817.3 (2250.7)	0.0	0.0	-	0.0
Basal area other trees	1847.8 (1586.2)	636.7 (938.7)	7.5 (47.2)	-	334.6 (703.2)

FIG. 1. Map of study area and location of sample sites on Sapelo Island, McIntosh County, Georgia and the Clayhole Swamp in Glynn County, Georgia.

FIG. 2. Indicator Value (IV) scores for species in each of five habitats in coastal Georgia, USA. Also shown is the indicator cutoff value (25) of Dúfrêne and Legendre (1997). * = Species that also had significantly higher densities using distance-sampling methods. Northern Mockingbird (in italics) IV score was not significant. (YTWA = Yellow-throated Warbler, NOPA = Northern Parula, WEVI = White-eyed Vireo, GCFL = Great-created Flycatcher, EAWP = Eastern Wood-pewee, CARW = Carolina Wren, YTVI = Yellow-throated Vireo, BGGN = Blue-gray Gnatcatcher, CACH = Carolina Chickadee, BHNU = Brown-headed Nuthatch, PIWA = Pine Warbler, RBWO = Red-bellied Woodpecker, EABL = Eastern Bluebird, RHWO = Red-headed Woodpecker, MODO = Mourning Dove, COYE = Common Yellowthroat, BLJA = Bluejay, BRTH = Brown Thrasher, CLRA = Clapper Rail, RWBL = Red-winged Blackbird, BTGR = Boat-tailed Grackle, MAWR = Marsh Wren, EAKI = Eastern Kingbird, WHIM = Whimbrel, GREG = Greg Egret, SESP = Seaside Sparrow, WILL = Willet, RUTU = Ruddy Turnstone, WIPL = Wilson's Plover, PABU = Painted Bunting, EATO = Eastern Towhee, YBCH = Yellow-breasted Chat, NOCA = Northern Cardinal, BHCO = Brown-headed Cowbird, OROR = Orchard Oriole, BLGR = Blue Grosbeak, COGD = Common Ground-Dove, NOMO = Northern Mockingbird, REVI = Red-eyed Vireo, HOWA = Hooded Warbler, YBCU = Yellow-billed Cuckoo, PROT = Prothonotary Warbler, ACFL = Acadian Flycatcher, ETTI = Eastern Tufted Titmouse, PIWO = Pileated Woodpecker, SUTA = Summer Tanager, RSHA = Red-shouldered Hawk, BDOW = Barred Owl, and YCNH = Yellow-crowned Night Heron).

FIG. 3. Biplot of sample sites (a) and bird species (b) intra-set LC scores (scores constrained to the environmental space by regressing the weighted species scores against the environmental variables) in coastal Georgia during the summers of 2006 and 2007 using canonical correspondence analysis (CCA) space constrained by habitat characteristics. Species in (b) are grouped by their ISA status. Vector lengths indicate the relative importance of each habitat characteristic on the ordination axes. Beginning with the right-pointing vector and going clockwise, the vectors are: 1) % herbaceous cover, 2) sapling height, 3) % litter cover, 4) % forest cover, 5) basal area other tree species, and 6) basal area tupelo gum. Species abbreviations follow American Ornithologists' Union alpha codes available at http://www.pwrc.usgs.gov/bbl/manual/bandsize.htm.

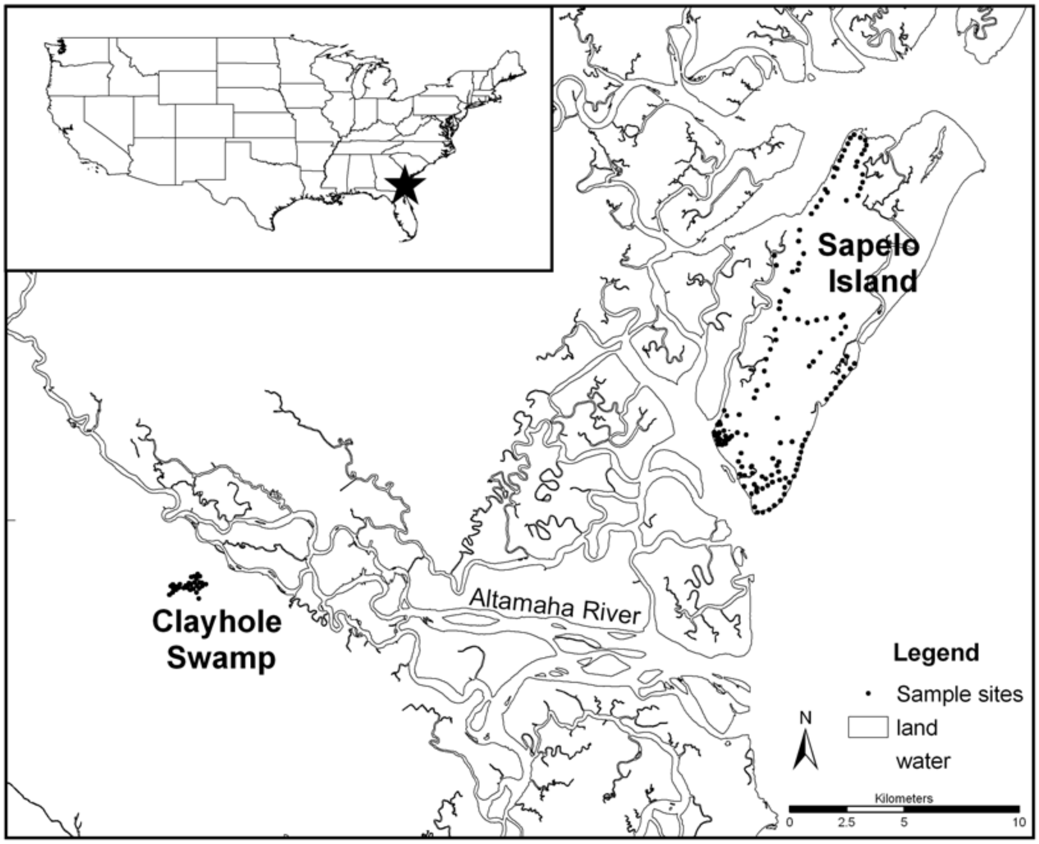
Sapelo Island
Clayhole Swamp
Altamaha River
Legend
Sample sites
land
water
N
Kilometers
0
2.5
5
10

Figure 1.

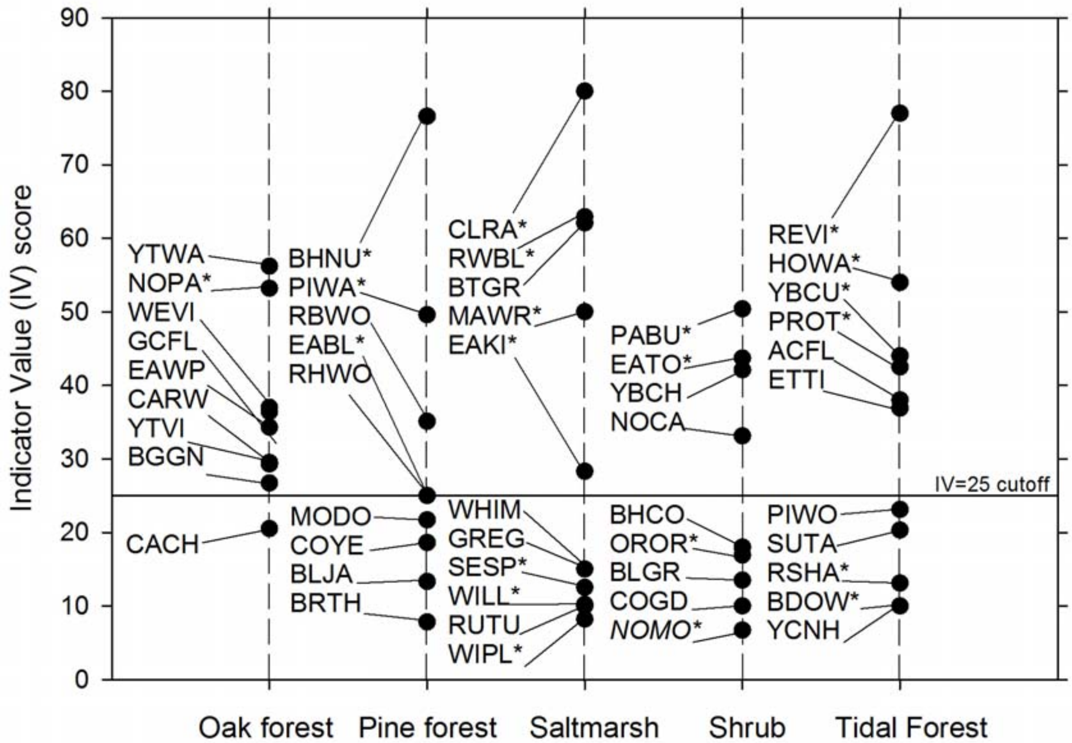
Indicator Value (IV) score
90
80
70
60
50
40
30
20
10
0
YTWA
NOPA*
WEVI
GCFL
EAWP
CARW
YTVI
BGGN
CACH
BHNU*
PIWA*
RBWO
EABL*
RHWO
MODO
COYE
BLJA
BRTH
CLRA*
RWBL*
BTGR
MAWR*
EAKI*
WHIM
GREG
SESP*
WILL*
RUTU
WIPL*
PABU*
EATO*
YBCH
NOCA
BHCO
OROR*
BLGR
COGD
NOMO*
REVI*
HOWA*
YBCU*
PROT*
ACFL
ETTI
PIWO
SUTA
RSHA*
BDOW*
YCNH
IV=25 cutoff
Oak forest
Pine forest
Saltmarsh
Shrub
Tidal Forest

Figure 2.

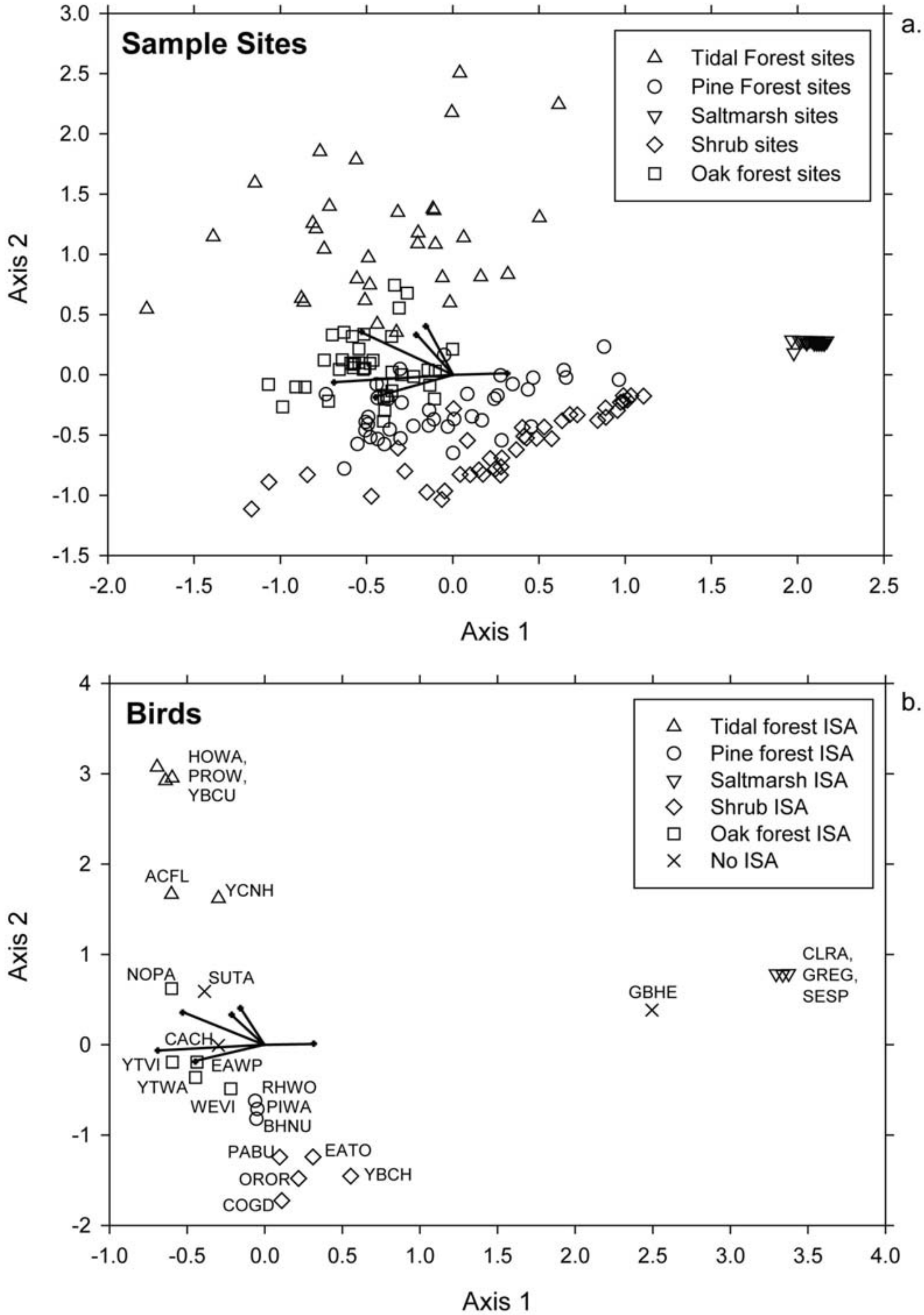
a.
Sample Sites
Tidal Forest sites
Pine Forest sites
Saltmarsh sites
Shrub sites
Oak forest sites
Axis 1
Axis 2
b.
Birds
Tidal forest ISA
Pine forest ISA
Saltmarsh ISA
Shrub ISA
Oak forest ISA
No ISA
HOWA,
PROW,
YBCU
ACFL
YCNH
NOPA
SUTA
CLRA,
GREG,
SESP
GBHE
CACH
YTVI
EAWP
YTWA
WEVI
RHWO
PIWA
BHNU
PABU
EATO
OROR
YBCH
COGD
Axis 1
Axis 2

Figure 3.

Appendix 1. Habitat characteristics in saltwater marshes of Sapelo Island, Georgia. Measurements are in meters except where. Stem density is in number of stems/m^2, herb height is in cm, and area is in m^2. Upland = distance to the nearest upland edge. Water = distance to the nearest water. Patch = distance to the nearest patch > 40 ha.

Site	Year	Upland	Water	Area	Perimeter	Patch	% herb	Herb height	Stems	Herb stem density
32	2006	311	114	147.7	11647	377	85	73	75	150
32	2007	311	114	147.7	11647	377	45	55	38	76
33	2006	535	15	147.7	11647	588	80	81	48	96
33	2007	535	15	147.7	11647	588	90	116	36	72
34	2006	76	54	54.8	7876	166	95	130	57	114
34	2007	76	54	54.8	7876	166	80	99	40	80
35	2006	45	24	25.6	2541	221	75	84	47	94
35	2007	45	24	25.6	2541	221	45	83	45	90
36	2006	137	19	57.7	7795	249	85	98	67	134
36	2007	137	19	57.7	7795	249	70	75	46	92
37	2006	94	8	147.7	11647	802	95	92	70	140
37	2007	94	8	147.7	11647	802	55	71	61	122
38	2006	432	38	147.7	11647	1004	85	95	61	122
38	2007	432	38	147.7	11647	1004	80	85	58	116
39	2006	21	18	147.7	11647	730	90	104	56	112
39	2007	21	18	147.7	11647	730	65	80	58	116
40	2006	65	38	57.7	7795	177	75	86	39	78

40	2007	65	38	57.7	7795	177	35	49	39	78
41	2006	71	61	57.7	7795	320	60	80	47	94
41	2007	71	61	57.7	7795	320	75	68	57	114
93	2007	33	17	147.7	11647	54	60	61	63	126
94	2007	28	24	147.7	11647	61	75	69	74	148
95	2007	178	106	147.7	11647	126	50	71	53	106
96	2007	22	253	147.7	11647	466	35	95	31	62
97	2007	51	312	147.7	11647	756	20	38	87	174
98	2007	120	31	57.7	7795	426	70	42	74	148
99	2007	43	68	54.8	7876	91	55	49	71	142
100	2007	98	27	54.8	7876	156	55	54	34	68
101	2007	153	38	54.8	7876	312	65	44	56	112
102	2007	292	102	54.8	7876	449	65	66	48	96
103	2007	17	36	57.7	7795	528	90	69	81	162
104	2007	34	142	57.7	7795	712	80	89	43	86
105	2007	185	412	147.7	11647	579	45	37	83	166
106	2007	68	203	144.8	10958	134	45	30	126	252
107	2007	236	38	144.8	10958	221	60	58	36	72
108	2007	49	731	14.2	2777	845	40	39	54	108
109	2007	30	77	14.2	2777	159	50	104	29	58
110	2007	72	31	3.3	775	236	75	86	39	78
111	2007	110	45	6.8	2581	80	55	70	36	72
112	2007	213	23	7.0	1760	331	75	85	43	86

Appendix 2. Habitat characteristics in maritime scrub-shrub on Sapelo Island, Georgia. Measurements are in meters except where noted as percent. Stem densities are in number of stems/m^2, herb height is in cm, and basalarea is in cm^2. Broad = broadleaf trees, narrow = narrowleaf trees, herb = herbaceous plants. Edge = distance to the nearest edge. Water = distance to the nearest water. Patch = distance to the nearest patch > 40 ha.

Site	Year	Edge	Water	Patch	% broad	% narrow	Broad height	Narrow height	Tree stem density	% sub-canopy	Sub-canopy height	% sapling	% dead sapling	Sapling height	Sapling stem density	% herb	% litter	Herb height	Basalarea
1	2006	154	340	3630	0	5	0.0	10.0	0.03	40	10.0	5	0	8.5	0.08	95	95	85	1930.5
1	2007	154	340	3630	0	0	0.0	0.0	0.00	0	0	38	0	9.5	0.08	85	55	85	1875.9
2	2006	147	320	3980	5	0	7.5	0.0	0.01	10	7.5	40	0	3.5	0.01	90	95	103	452.4
2	2007	147	320	3980	5	0	7.5	0.0	0.01	5	7.5	40	0	3.8	0.31	80	65	103	683.5
3	2006	35	86	4029	3	15	21.0	13.0	0.04	30	14.0	50	0	4.6	0.08	65	95	116	2351.5
3	2007	35	86	4029	0	15	0.0	14.0	0.04	15	14	70	0	5.5	0.06	45	55	116	2433.2
4	2006	12	341	4542	0	15	0.0	15.0	0.04	25	14.0	35	0	5.0	0.43	40	90	125	1361.3
4	2007	12	341	4542	0	15	0.0	15.5	0.04	15	15.5	50	0	6.0	0.37	35	60	125	1407.8
7	2006	16	615	2056	5	5	7.5	11.0	0.01	15	11.5	75	0	2.5	0.97	40	85	120	1256.6
7	2007	16	615	2056	5	0	7.5	0.0	0.01	5	7.5	85	0	3.6	0.94	45	70	120	1320.3
19	2006	65	767	1256	0	0	20.0	0.0	0.04	20	17.8	70	0	3.5	1.40	25	75	76	2830.2
26	2006	178	178	1957	0	5	0.0	4.0	0.03	10	7.5	40	0	2.5	0.28	35	99	96	1550.6

26	2007	178	178	1957	0	10	0.0	6.0	0.03	10	6	55	0	3.5	0.39	45	75	96	1678.4
27	2006	450	1622	1312	0	3	0.0	12.5	0.00	5	12.0	50	0	3.5	0.53	70	70	140	0.0
27	2007	143	1622	1312	0	3	0.0	13.0	0.00	3	13	45	0	3.6	0.52	40	60	140	0.0
29	2006	67	303	1800	0	5	0.0	10.5	0.00	30	10.5	65	0	3.0	0.56	90	80	93	0.0
29	2007	67	303	1800	0	10	0.0	12.5	0.00	10	12.5	55	0	2.5	0.69	15	25	93	0.0
30	2006	82	251	2229	0	3	0.0	9.0	0.00	10	9.0	70	5	3.0	0.60	20	95	68	0.0
30	2007	82	251	2229	0	5	0.0	10.0	0.00	5	10	40	0	3.0	0.59	5	15	68	0.0
113	2007	159	210	1491	0	10	0.0	15.0	0.00	10	15	55	0	2.5	0.62	5	65	71	0.0
114	2007	64	207	1171	0	5	0.0	15.5	0.00	5	15.5	35	5	3.0	0.65	20	15	42	0.0
115	2007	101	158	841	0	5	0.0	10.0	0.00	5	10	60	10	3.5	0.61	5	45	51	0.0
116	2007	65	179	543	0	10	0.0	9.5	0.06	10	9.5	30	15	4.5	0.11	10	55	68	802.5
117	2007	135	284	2538	0	0	0.0	0.0	0.01	0	0	35	0	4.5	0.08	20	15	22	122.7
118	2007	199	199	4297	0	0	0.0	0.0	0.01	0	0	45	0	3.5	0.27	40	15	94	132.7
119	2007	167	167	4647	0	0	0.0	0.0	0.00	0	0	55	0	4.5	0.31	35	15	97	0.0
120	2007	203	203	4954	0	0	0.0	0.0	0.00	0	0	45	10	4.5	0.33	20	33	99	0.0
121	2007	101	101	5227	0	0	0.0	0.0	0.00	0	0	40	30	3.5	0.08	55	45	136	0.0
122	2007	68	68	5400	0	0	0.0	0.0	0.00	0	0	25	40	4.5	0.17	30	20	140	0.0
123	2007	109	109	5535	0	0	0.0	0.0	0.00	0	0	35	25	5.0	0.27	35	20	109	0.0
124	2007	120	120	5380	0	0	0.0	0.0	0.01	0	0	40	0	2.5	0.10	55	40	100	103.9

125	2007	82	247	3754	0	0	0.0	0.0	0.01	0	0	45	0	2.5	0.18	45	30	99	283.5
126	2007	119	119	3403	0	0	0.0	0.0	0.00	0	0	33	10	3.0	0.24	45	15	89	0.0
127	2007	212	212	3113	0	0	0.0	0.0	0.00	0	0	30	0	2.7	0.22	45	30	92	0.0
128	2007	224	224	2847	0	0	0.0	0.0	0.00	0	0	33	15	3.0	0.29	55	35	63	0.0
129	2007	177	177	2574	0	0	0.0	0.0	0.00	0	0	75	0	3.2	0.33	10	65	76	0.0
130	2007	152	152	2283	0	0	0.0	0.0	0.00	0	0	38	10	3.0	0.22	20	25	111	0.0
132	2007	169	169	1670	0	10	0.0	11.5	0.03	10	11.5	65	5	4.5	0.10	45	40	99	1572.8
133	2007	190	190	1399	0	15	0.0	11.5	0.03	15	11.5	45	5	3.5	0.13	25	45	107	644.8
134	2007	34	112	3821	35	0	16.8	0.0	0.04	35	16.8	70	0	9.5	0.15	35	60	58	1802.7

Appendix 3. Habitat characteristics in maritime broadleaf forest on Sapelo Island, Georgia. Measurements are in meters except where noted as percent. Stem densities are in number of stems/m^2, herb height is in cm, and basalarea is in cm^2. Broad = broadleaf trees, narrow = narrowleaf trees, herb = herbaceous plants. Pine = distance to the nearest narrowleaf forest edge. Water = distance to the nearest water. Patch = distance to the nearest patch > 40 ha.

Site	Year	Pine	Water	Patch	% forest	% broad	% narrow	Broad height	Narrow height	Tree stem density	% sub-canopy	Sub-canopy height	% sapling	Sapling height	Sapling stem density	% herb	% litter	Herb height	Basalarea
5	2006	139	436	2685	95	65	30	23.0	33.0	0.06	35	11.0	5	2.3	0.06	10	99	30	15759.4
5	2007	139	436	2685	85	65	20	23.0	33.0	0.06	35	11.0	3	2.3	0.04	3	99	30	15799.3
11	2006	180	1104	3104	80	75	5	26.0	26.0	0.05	15	8.5	20	4.0	0.05	10	99	62	5765.2
11	2007	180	1104	3104	85	75	10	26.0	26.0	0.04	15	8.5	20	4.5	0.04	5	99	62	5835.7
13	2006	177	477	4493	75	50	25	22.0	28.5	0.09	35	11.0	5	3.5	0.14	30	99	51	3817.2
13	2007	177	477	4493	85	65	20	22.0	28.5	0.09	15	10.5	5	3.5	0.14	3	99	51	3915.6
14	2006	400	133	4194	95	92	3	25.5	31.5	0.09	15	11.5	5	2.5	0.14	10	98	49	3160.0
14	2007	400	133	4194	90	85	5	25.5	31.5	0.09	15	11.5	10	2.0	0.13	3	100	49	3559.8
15	2006	221	117	3456	85	80	5	26.0	26.5	0.04	15	11.5	15	2.0	0.10	0	99	0	2644.6
15	2007	221	117	3456	85	75	10	26.0	26.5	0.04	15	11.5	5	2.0	0.05	2	100	33	2659.8
16	2006	159	430	3310	75	75	0	28.5	0.0	0.04	45	9.5	85	2.0	0.33	0	95	0	2510.3
16	2007	159	430	3310	70	70	0	28.0	0.0	0.03	45	9.5	80	3.5	0.32	2	95	48	2553.5

17	2006	99	367	3020	90	85	5	32.0	34.0	0.04	30	12.5	25	3.0	0.36	10	99	52	9275.7
17	2007	99	367	3020	80	70	10	32.0	34.0	0.05	30	12.5	25	3.5	0.09	5	99	52	9486.0
23	2006	76	247	5538	90	85	5	25.5	28.5	0.03	10	11.5	10	3.0	0.15	60	90	58	10339.8
23	2007	76	247	5538	90	85	5	25.5	28.5	0.03	10	11.5	10	2.5	0.10	25	99	58	10429.5
24	2006	524	245	6158	90	75	15	23.5	32.5	0.05	15	9.5	50	2.5	0.23	40	95	53	6036.2
24	2007	524	245	6158	75	60	15	23.5	32.5	0.05	15	9.5	45	2.5	0.22	35	95	53	6219.8
25	2006	311	151	6619	80	75	5	23.0	14.5	0.04	40	12.5	25	3.0	0.15	15	95	41	9635.9
25	2007	311	151	6619	60	55	5	23.0	14.5	0.04	40	12.5	25	1.4	0.11	15	95	44	10371.2
52	2007	155	198	6780	55	55	0	28.5	0.0	0.03	15	10.5	60	2.0	0.11	35	90	123	5321.3
53	2007	127	159	7002	65	45	20	25.5	33.0	0.06	55	12.5	30	2.5	0.17	20	95	112	2783.8
54	2007	88	194	7217	90	80	10	24.0	28.5	0.03	25	10.0	15	2.5	0.14	10	95	58	3698.4
55	2007	178	134	7523	70	65	5	29.0	29.5	0.03	10	11.5	15	1.5	0.05	25	99	49	6035.8
56	2007	189	171	7861	70	65	5	29.0	34.0	0.03	20	12.5	25	2.0	0.13	20	95	56	2809.4
57	2007	200	149	8157	80	75	5	25.5	27.5	0.04	10	13.5	15	2.5	0.13	5	98	50	3875.2
58	2007	142	196	8317	65	65	0	25.0	0.0	0.05	15	11.5	10	2.0	0.06	35	90	50	9897.0
59	2007	96	150	8291	55	53	2	16.0	22.5	0.03	5	9.0	75	2.5	0.19	2	95	24	3480.3
60	2007	95	112	8289	70	45	25	26.0	27.5	0.03	5	10.0	20	2.5	0.15	45	95	54	1608.5
61	2007	76	307	8076	85	75	10	21.5	26.5	0.03	5	10.0	15	2.5	0.09	15	99	43	6758.4
62	2007	109	370	7860	75	70	5	23.0	34.0	0.05	5	10.5	35	2.2	0.05	15	99	41	8990.6
63	2007	102	350	7624	65	62	3	26.5	27.5	0.03	10	8.5	15	2.0	0.08	5	99	38	4305.0

65	2007	114	323	6994	50	45	5	21.0	23.5	0.04	15	12.0	65	2.5	0.18	5	98	96	6325.6
66	2007	487	163	6819	65	40	25	28.5	26.0	0.01	30	8.5	40	2.0	0.14	45	90	46	2083.1
67	2007	751	241	6556	85	65	20	22.0	25.5	0.04	5	10.5	20	1.8	0.05	25	99	54	4639.7
68	2007	956	392	6232	60	35	25	25.5	31.0	0.03	25	10.5	20	1.5	0.14	25	90	52	1958.2
69	2007	827	350	5913	65	45	20	22.5	31.0	0.04	10	10.5	10	2.0	0.10	1	98	33	809.5
71	2007	263	558	5524	70	65	5	23.5	27.0	0.04	15	7.5	45	2.9	0.08	20	85	61	3276.3
74	2007	161	409	4667	90	75	15	30.5	30.0	0.01	45	13.0	15	3.0	0.15	20	95	91	16741.5
76	2007	143	607	1666	80	65	15	32.0	34.0	0.04	15	12.5	35	4.5	0.22	30	99	82	9892.5

Appendix 4. Habitat characteristics in maritime narrowleaf forest on Sapelo Island, Georgia. Measurements are in meters except where noted as percent. Stem densities are in number of stems/m^2, herb height is in cm, and basalarea is in cm^2. Broad = broadleaf trees, narrow = narrowleaf trees, herb = herbaceous plants. Oak = distance to the nearest broadleaf forest edge. Water = distance to the nearest water. Patch = distance to the nearest patch > 40 ha.

Site	Year	Oak	Water	Patch	% forest	% broad	% narrow	Broad height	Narrow height	Tree stem density	% sub-canopy	Sub-canopy height	% sapling	Sapling height	Sapling stem density	% herb	% litter	Herb height	Basalarea
6	2006	262	1083	12678	80	10	70	34.0	34.0	0.10	45	12.5	15	3.5	0.09	35	99	52	7955.9
6	2007	262	1083	12678	65	5	60	34.5	34.5	0.10	45	12.5	3	2.2	0.01	3	99	52	8423.0
9	2006	71	703	10280	55	10	45	32.3	32.3	0.09	25	13.0	5	2.0	0.10	70	99	40	7761.9
9	2007	71	703	10280	70	15	55	20.4	31.5	0.06	25	13.0	15	3.0	0.05	5	85	40	7431.6
10	2006	56	486	10632	60	15	45	31.4	31.4	0.09	15	16.5	3	2.0	0.01	25	99	32	7851.2
10	2007	56	486	10632	55	5	50	31.2	31.2	0.08	15	16.5	15	4.0	0.04	3	70	32	6838.1
12	2006	67	181	229	30	2	28	34.2	34.2	0.04	20	9.0	20	4.0	0.18	15	99	230	4280.8
12	2007	67	181	229	50	5	45	29.8	39.8	0.03	20	9.0	40	3.5	0.05	35	95	230	3363.1
18	2006	112	354	6525	55	0	55	0.0	32.5	0.03	35	9.5	65	3.0	0.62	25	99	46	4512.9
18	2007	112	354	6525	55	5	50	32.5	32.5	0.04	35	9.5	65	3.0	0.24	10	95	46	4701.8
20	2006	508	959	4891	25	0	25	0.0	28.1	0.03	5	13.5	3	1.5	0.03	95	95	42	2664.1
20	2007	508	959	4891	45	0	45	0.0	28.5	0.03	5	13.5	3	2.0	0.01	80	95	42	2676.8

21	2006	312	777	4103	25	0	25	0.0	26.1	0.01	5	13.0	40	3.0	0.52	95	90	64	3525.7
21	2007	312	777	4103	45	0	45	0.0	26.0	0.01	5	13.0	40	4.0	0.36	85	80	64	3848.5
22	2006	413	545	315	45	5	40	32.5	32.5	0.01	10	9.5	35	3.0	0.20	85	90	107	2375.8
22	2007	413	545	315	40	0	40	0.0	33.5	0.03	10	9.5	55	2.5	0.20	45	65	107	2630.3
28	2006	278	532	347	40	3	37	27.5	27.5	0.04	10	13.0	30	3.0	0.27	20	95	53	4461.3
28	2007	278	532	347	45	2	43	27.5	27.5	0.03	10	13.0	35	3.5	0.09	35	95	53	4359.9
31	2006	260	392	11940	85	0	85	0.0	37.3	0.09	55	12.5	10	2.0	0.10	70	99	41	2358.6
31	2007	260	392	11940	75	0	75	0.0	35.0	0.11	55	12.5	3	1.2	0.01	3	85	41	2524.5
64	2007	77	257	1734	45	2	43	23.0	23.5	0.01	5	12.5	80	2.0	0.20	5	75	39	1809.6
72	2007	101	404	1169	40	0	40	0.0	27.0	0.01	5	13.0	85	3.5	0.20	55	45	68	1772.1
73	2007	242	375	1597	40	10	30	22.5	27.5	0.01	15	18.5	20	3.0	0.08	55	45	84	1486.2
75	2007	309	391	161	40	0	40	0.0	29.5	0.03	5	9.0	40	4.0	0.39	15	90	70	2716.3
77	2007	252	836	4648	45	0	45	0.0	29.5	0.01	5	15.0	5	1.5	0.03	90	98	50	2083.1
78	2007	686	743	5957	40	15	25	17.5	27.5	0.04	25	11.5	55	3.5	0.24	60	90	86	2412.4
79	2007	242	42	254	15	0	15	0.0	27.8	0.01	5	12.5	30	3.2	0.14	70	55	123	1734.9
80	2007	336	959	9018	33	0	33	0.0	24.5	0.03	25	9.5	20	3.0	0.22	15	55	117	1003.9
81	2007	423	981	8758	50	0	50	0.0	29.5	0.03	10	8.5	12	2.0	0.18	30	65	38	1467.5
82	2007	188	932	8344	45	0	45	0.0	27.5	0.03	10	8.0	45	2.2	0.18	80	33	109	1189.5
83	2007	83	575	7684	40	0	40	0.0	30.0	0.03	5	8.0	5	2.0	0.14	65	65	83	510.5

84	2007	101	523	7404	45	0	45	0.0	25.0	0.04	35	9.5	55	3.0	0.14	70	85	42	2131.6
85	2007	67	614	7080	35	0	35	0.0	25.0	0.03	15	18.5	40	1.5	0.11	40	55	39	1318.1
86	2007	399	919	6536	45	0	45	0.0	28.5	0.03	5	12.5	15	1.0	0.09	65	65	51	2724.5
87	2007	532	960	6641	35	5	30	26.0	30.5	0.04	45	12.5	25	4.5	0.32	10	75	55	4010.6
88	2007	1095	1511	6755	25	0	25	0.0	25.2	0.03	25	11.5	20	1.5	0.34	75	45	40	508.9
89	2007	870	1655	6871	30	0	30	0.0	29.5	0.04	35	12.0	80	1.5	0.22	15	85	36	2793.1
90	2007	592	1689	7062	35	5	30	16.5	29.5	0.05	50	12.5	55	3.0	0.55	3	95	37	587.7
91	2007	525	1275	7052	50	0	50	0.0	22.5	0.04	3	9.5	25	3.5	0.23	15	90	38	2482.6
92	2007	177	802	7162	30	0	30	0.0	26.5	0.04	55	12.5	25	2.5	0.47	3	80	39	2100.5

Appendix 5. Total point count detections and bird banding captures of target species at the same sample sites in coastal Georgia, with mean and standard deviation. BHNU and RBWO were in maritime narrowleaf forest, PABU and WEVI were in maritime scrub-shrub, CARW was in tidal freshwater forest and YTWA was in maritime broadleaf forest.

Species	Point Count Detections			Bird Banding Captures		
	Total	Mean	SD	Total	Mean	SD
BHNU	37	1.9	1.1	48	2.4	1.6
CARW*	33	1.7	0.7	13	0.7	0.5
NOPA (broadleaf forest)	52	2.6	0.9	60	3.0	1.4
NOPA (tidal freshwater forest)	26	1.3	0.7	21	1.1	1.1
PABU	24	1.1	0.9	28	1.3	1.5
RBWO*	39	1.9	0.6	11	0.5	0.7
WEVI	38	1.7	1.1	61	2.8	2.1
YTWA*	44	2.2	1.2	23	1.2	1.1

* = Point count detections significantly higher than bird banding captures using Mann-Whitney U-tests (P<0.05).

Comparing point count detections to the captures of target species shows that no species were captured at higher rates than detected. However, three species were captured at significantly lower rates than detected on point counts (Carolina Wrens: $U = 554.5$, n = 20, $P < 0.0005$; Red-bellied Woodpeckers: $U = 630.5$, n = 21, $P < 0.0005$; and Yellow-throated Warblers: $U = 515.5$, n = 20, $P = 0.0028$).

SENSITIVITY ANALYSIS OF AVIAN FOOD WEB CHARACTERIZATION USING ISOSOURCE AND STABLE ISOTOPES OF ^{13}C AND ^{15}N

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Abstract. This study traced the base food web and invertebrate consumption of birds on Sapelo Island and in the Clayhole Swamp of coastal Georgia using $\delta^{13}C$ and $\delta^{15}N$ stable isotopic signatures of plants, invertebrates and bird feathers. *Isosource* 1.3.1 mixing models of primary production sources were successful on Sapelo Island where there were large differences in photosynthetic pathways and hydrology, but failed in the Clayhole Swamp where there was one photosynthetic pathway and hydrologic condition. This study is among the first to show that stable isotopes can be used to trace passerine food webs not only for primary production sources but also invertebrate sources. Model sensitivity analysis indicated that both the trophic level and isotopic enrichment of the organisms had a greater effect on modeled results than the internal variability of *Isosource* models. Studies tracing primary production sources will need accurate approximations of trophic level to account for trophic isotopic enrichment or should conduct similar sensitivity analyses to determine the best estimate. Primary production models had less source partitioning variability due to different parameters than prey source models, indicating that species specific trophic enrichment values are needed to accurately partition prey items.

Keywords: carbon isotopes, nitrogen isotopes, Isosource, sensitivity analysis, Georgia, avian food web, trophic position, Sapelo Island, passerine, rail, screech owl

INTRODUCTION

Stable isotope studies have become increasingly important to assess animal trophic webs, while simultaneously showing that isotopic trophic signatures vary with species and tissue type (Peterson and Fry 1987, Hobson et al. 1994, Hobson 1999, Harding and Stevens 2001, Post 2002, Pearson et al. 2003, Langellotto et al. 2005). Tissue samples used in isotopic trophic analyses, such as feathers or bone collagen, must have grown on young of yearly derived food in the habitat and during the time period of interest (Bearhop et al. 2004). Potential food sources within the trophic web must also exhibit diagnostic isotopic differences that are temporally stable during the study period (Peterson and Fry 1987, Bearhop et al. 2004).

Potential food sources of animals in trophic studies are partitioned using mixing models (Phillips et al. 2005, Ramos et al. 2009). However, in order for sources to be partitioned, researchers must know important parameters, such as the relative trophic position, the trophic effect on isotopic signatures, and the sensitivity of these parameters to source partition models.

The stable isotopic composition of avifauna tissues, including feathers, reflects the mean value of each stable isotope ratio found in source materials used to grow the tissues, such as food ingested during the period of tissue growth and stored biomass (Duxbury and Holroyd 1997). The ratios of $^{13}C/^{12}C$ in feathers (expressed as $\delta^{13}C$ values in ‰ units, or ppt) relative to international standards can be used to infer avian food sources due to differences in $\delta^{13}C$ values between C_3, CAM and C_4 photosynthetic pathways (Bearhop et al. 2004). Primary production reaches birds through either direct herbivory or transformed invertebrate biomass, with varying ^{13}C-enrichment rates at different trophic levels that must be accounted for separately (Kelly 2000, Pearson et al. 2003). Animals typically increase $\delta^{13}C$ in whole body tissues by ~0.5‰ for each trophic level in their diet (Post 2002), ranging from no enrichment to as much as 1.6‰ in invertebrates (Langellotto et al. 2005). The amount of $\delta^{13}C$ increase varies in different types of body tissues at different time scales, with bone collagen typically ^{13}C-enriched by 2-6‰ and lipids ^{13}C-depleted by 2-8‰ (Peterson and Fry 1987). A recent study of Yellow-rumped Warblers (*Dendroica coronate* (Linnaeus 1766)) showed feathers ^{13}C-enriched by 1.9‰ when insects were a small part of their diet and up to 4.3‰ with nearly all insects (Pearson et al. 2003), indicating isotopic enrichment is positively correlated to the level of insectivory. Nitrogen stable isotope ratios ($\delta^{15}N$) show a similar systematic 3-5‰ ^{15}N-enrichment with each increase in trophic level. The ^{15}N-enrichment is less variable among body tissues than ^{13}C-enrichment and reveals information about an organism's trophic position (e.g. primary or secondary consumer; Peterson et al. 1985, Ambrose 1993, Harding and Stevens 2001).

Determining the relative proportion of different food sources typically involves source partitioning using linear mass balance equations (Phillips et al. 2005). However, linear equations are useless when the number of potential sources is greater than the number of isotopes analyzed by more than one, creating too many unknown quantities for the number of equations. In such cases, *Isosource* 1.3.1 (available at: http://www.epa.gov/wed/pages/models/stableIsotopes/isosource/isosource.htm) has the ability to analyze all of the potential source partition models that satisfy the mass balance between the sources and the organism(s), giving the mean, range and standard deviation of the potential solutions (Phillips et al. 2005). Each food source must first be corrected for trophic isotopic enrichment in order for the model to work appropriately (Phillips et al. 2005). Without accurate knowledge of trophic levels or enrichment, isotopic analysis may inaccurately estimate the proportional importance of dietary sources. Importantly, while sensitivity analysis has been conducted on the tolerance settings within *Isosource*, there is little published research on *Isosource* sensitivity to the trophic level and enrichment parameters (Phillips and Gregg 2003).

This study assesses the ability of *Isosource* to partition primary production sources and prey items in avian food webs for at least two target bird species (ten total) in each of five habitats in coastal Georgia, USA [Clapper Rail (*Rallus longirostris* (Boddeart, 1783)), Eastern Screech Owl (*Megascops asio* (Linnaeus, 1758)), Red-bellied Woodpecker (*Melanerpes carolinus* (Linnaeus, 1758)), White-eyed Vireo (*Vireo griseus* (Boddeart, 1783)), Brown-headed Nuthatch (*Sitta pusilla* (Latham, 1790)), Carolina Wren (*Thryothorus ludovicianus* (Latham, 1790)), Marsh Wren (*Cistothorus palustris* (A. Wilson, 1810)), Northern Parula (*Parula americana* (Linnaeus, 1758)), Yellow-throated Warbler (*Dendroica dominica* (Linnaeus, 1766)), and Painted Bunting (*Passerina ciris* (Linnaeus, 1758))]. The study first determines the ability of stable isotopes and *Isosource* mixing models to characterize passerine trophic food webs in small geographic areas. Lastly, the study analyses *Isosource* sensitivity to model trophic position and enrichment parameters by analyzing a range of possible mixing solutions to isotopic source partitions.

METHODS

Study Area

Five habitats of coastal Georgia, USA, were sampled: tidal-freshwater broadleaf deciduous forest, saltmarsh, maritime scrub-shrub, maritime broadleaf evergreen forest, and maritime narrowleaf evergreen forest (Figure 1). The tidal-freshwater forest (tidal forest) sites are located in the Clayhole Swamp Wildlife Management Area in Glynn County, Georgia, owned and managed by the Georgia Department of Natural Resources, and were dominated by bald cypress (*Taxodium distichum* (L.) Rich.) and tupelo gum (*Nyssa aquatic* L.). Saltmarsh, maritime scrub-shrub (shrub), maritime broadleaf evergreen forest (oak forest) and maritime narrowleaf evergreen forest (pine forest) were sampled on 6,677 ha Sapelo Island, McIntosh

County, Georgia, on property jointly owned and managed by the Georgia Department of Natural Resources and the Sapelo Island National Estuarine Research Reserve. See Brittain et al. (2009) for a detailed description of the sample points.

Vegetation sampling

Vegetation was sampled at each site by collecting whole stems of growing herbaceous plants or by clipping small branches of live woody vegetation. Samples were placed in zip-lock bags and placed on ice in the field. Sampled species of plants included live oak (*Quercus virginiana* P. Mill.), American holly (*Ilex opaca* Ait.), Spanish moss (*Tillandsia usneoides* (L.) L.) and redbay (*Persea borbonia* (L.) Spreng.) in oak forest. Loblolly pine (*Pinus taeda* L.) , slash pine (*Pinus elliottii* Engelm.), wax myrtle (*Morella cerifera* (L.) Small), yaupon (*Ilex vomitoria* Ait.), and saw palmetto (*Serenoa repens* (Bartr.) Small) were sampled in pine forest. Wax myrtle, yaupon, red cedar (*Juniperus virginiana* L.), *Andropogon* ssp., muhly grass (*Muhlenbergia filipes* M.A. Curtis) and dog fennel (*Eupatorium capillifolium* (Lam.) Small) were sampled in shrub habitat. Smooth cordgrass was sampled from the low saltmarsh zone closest to the tidal channels, while black needle rush (*Juncus roemerianus* Scheele), sea ox-eye (*Borrichia frutescens* (L.) DC.) and glasswort (*Salicornia virginica* L.) were sampled in the high saltmarsh zone closest to uplands. Plant species sampled in tidal forest were bald cypress, tupelo gum, sweet gum (*Liquidambar styraciflua* L.), water oak (*Quercus nigra* L.), blue palm (*Sabal minor* (Jacq.) Pers.), *Panicum* ssp. and lizard tail (*Saururus cernuus* L.). Berries were also sampled from wax myrtle, American holly, yaupon, lizard tail and red cedar.

Invertebrate sampling

Invertebrates were sampled at ten points in each habitat by sweeping plants with an insect net. An invertebrate sample event occurred at each point by constantly sweeping the outer foliage of multiple plants of the same species (up to 3 m) for three minutes. Fiddler crabs (*Uca* *pugnax* (S. I. Smith, 1870)) were sampled by hand at each of the saltmarsh sites. Sweep net contents from each plant species, and fiddler crabs, were placed in a zip-lock plastic bag, put into a cooler of ice in the field, and placed in a freezer at the end of the field day.

Bird Sampling

Ten sample points were located in each habitat type (50 total) in 2006. Capture and banding were attempted for at least two target species of birds in each habitat type. Target species include: Northern Parula and Carolina Wren in tidal forest; Marsh Wren and Clapper Rail in saltmarsh; Eastern Screech Owl, Painted Bunting and White-eyed Vireo in shrub; Eastern Screech Owl, Northern Parula and Yellow-throated Warbler in oak forest; and, Eastern Screech Owl, Brown-headed Nuthatch and Red-bellied Woodpecker in pine forest.

For all species, except Clapper Rails, banding included setting up one 12 m X 2.6 m mistnet (30-mm, 38-mm or 60-mm mesh, depending on species) at each of the 50 sample points and playing the conspecific song of each target species for 30 minutes. Conspecific songs were taken from the Stokes Field Guide to Bird Songs: Eastern Region (Elliott et al. 1997), and edited to remove the voiceover identification tag. Banding attempts occurred at least twice in 2006 during the period from May 22nd to July 13th with three weeks between banding attempts. All captured birds were identified to species, banded with sequentially numbered bands provided by the Bird Banding Laboratory, aged, sexed and measured for wing chord, tail length and mass. Eastern Screech Owls were captured within 3 hours after sunset from 20 June to 15 August in 2007. The ten sample points in each habitat were revisited twice between May 1st and July 15th in 2007 using the same techniques as in 2006.

Clapper Rails were captured using a 61 x 61 x 91 cm box funnel trap constructed with a wooden frame and 1.3 cm vinyl-coated hardware cloth. The box funnel trap was placed at the estimated high tide line to prevent drowning of birds in submerged traps. Drift fences were extended approximately 25 m on either side of the funnel trap down to the low tide line in a nearby tidal channel and into the short *Spartina alterniflora* of the marsh plain. Traps were checked after each high tide and captured Clapper Rails were processed using the banding techniques described above. Clapper Rails were captured from 2 July to 13 July in 2006 and from 1 July to 14 July in 2007.

Two outer retrices were sampled from every newly captured or recaptured bird with fresh feathers. Obviously fresh secondary feathers were sampled instead of obviously old retrices in order to obtain samples that were known to have grown on location during the study period. Feathers were placed in envelopes and stored in a dry, dark place until analyzed.

Stable isotope analysis

Feather samples were cleaned by ultrasonicating twice in a 2:1 vol:vol mixture of chloroform and methanol. Clean feathers were air dried, clipped and 1.2 – 1.5 mg of sample was weighed into tin capsules for analysis. Plant sample bags were freeze-dried, ground in a Wiley mill and 4.0 – 4.5 mg of sample was weighed into tin capsules. Most plants had atomic C:N ratios that prevented simultaneous $\delta^{13}C$ and $\delta^{15}N$ analyses due to instrument detection limits, in which case 8.0 – 10.0 mg were weighed for $\delta^{15}N$ analysis. Invertebrates' sample bags were also freeze-dried, sorted by family (Bland and Jacque 1978, Kaston 1978), and 1.5 – 1.8 mg of whole invertebrates were weighed for analysis. Fiddler crabs were ground, digested in 2 N hydrochloric acid solution at room temperature to decompose carbonate, washed with deionized water, and freeze-dried prior to analysis. Freeze-dried periwinkle snail (*Littoraria irrorata* (Say, 1822)) organic body parts were separated from the shell and ground for analysis.

Stable N- and C- isotopic compositions of feather, invertebrate and plant samples were determined using a Thermo-Finnigan Delta Plus XP isotope ratio mass spectrometer configured on-line with a Costech ECS4010 elemental analyzer at the Stable Isotope Research Facility, Department of Geological Sciences, Indiana University, Bloomington, Indiana. Samples in tin capsules were loaded into a Costech Zero Blank Autosampler. Samples were combusted in a cobaltous-cobaltic oxide furnace heated to 1020º C. Combustion gases were passed through a reduction furnace (elemental copper) heated to 650º C to convert NO_x to N_2. Helium carrier gas flow was 90 mL / min.

Measured $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios are expressed as $\delta^{13}C$ and $\delta^{15}N$ values in ‰ relative to air nitrogen and V-PDB, respectively. We use the common delta notation: $\delta X = (R_{sample}/R_{standard} - 1)*1000$, where X = the element of interest (e.g., C or N) and R = the ratio of the heavier isotope to the lighter isotope of element X (e.g., $^{13}C/^{12}C$ or $^{15}N/^{14}N$). Calibration is based on international stable isotope standards NBS 19, L-SVEC, IAEA-N-1 and IAEA-N-2, and on routinely run laboratory reference materials acetanilide and cornstarch which have been carefully calibrated using closed-tube combustion and vacuum line purification. See http://mypage.iu.edu/~aschimme/hc.html (section on materials for on-line EA-irm-MS) for additional method information. Acetanilide was the primary laboratory reference material used to calibrate sample isotopic ratios ($^{15}N/^{14}N$ and $^{13}C/^{12}C$) relative to international standards. Instrument error was estimated by the standard deviation of acetanilide $\delta^{13}C$ (relative to VPDB) and $\delta^{15}N$ (relative to air), which averaged 0.06‰ and 0.16‰, respectively.

Generally, each plant species and each invertebrate family that was captured in most of the sites (>50%) within a habitat was analyzed in triplicate each year. Sample size was insufficient for three samples of Thysanoptera in saltmarsh and Ortheziidae in oak forest. Invertebrates were grouped by feeding guild in each habitat for simplification of the analysis.

Statistics

The standard deviation of any given isotopic sample was propagated with the instrument error, and converted into a standard error.

Multi-Response Permutation Procedures (MRPP) were run in PC-ORD 5.0 for plants grouped by photosynthetic pathway (C_3, C_4 or CAM) in each habitat, and similar groups were combined until the isotopic signature of each group was different from the others (McCune and Grace 2002; Table 1). Each MRPP test in this study used Euclidean distance measures and weighted the groups by $n/\Sigma n$ (n = sample size). Invertebrates were grouped by feeding guild (according to Bland and Jacque 1978 and Kaston 1978) within each habitat and analyzed for differences using the same MRPP procedure as the plants (Table 2). The carnivore/parasite/omnivire (CPO) group included araneae, coleoptera (cleridae and coccinellidae), diptera (dolichopodidae), hemiptera (reduviidae), hymenoptera (braconidae, eurytomidae, formicidae, sphecidae and tiphiidae) and mantidae. Detritivores (D) were composed of blattaria, diplopoda, diptera (bibioniidae, culicidae and tipulidae), decapoda (*Uca pugnax*) and psocidae. The herbivore/fungivore (HF) group comprised the most variety of taxa; acarina, coleoptera (alleculidae, buprestidae, chrysomelidae, ciidae, curculionidae, elateridae, mordellidae and phalacridae), diptera (tephritidae), hemiptera (alydidae, aphididae, cercopidae, cicadellidae, cixiidae, delphacidae, flatidae, lygeaidae, miridae, ortheziidae and pentatomidae), lepidoptera, littorinidae (*Littoraria irrorata*), orthoptera and thysanoptera. Isotopic compositions of feather were grouped by species, habitat and age, and tested for differences using MRPP but with additional sequential-Bonferroni corrections to preserve 5% experimental error and a conservative distinction between avian species (Holm 1979; Table 3).

Source mixing models

Isosource 1.3.1 was used to estimate the percent contribution of each potential primary producer source to the food web of each avian species' habitat/age group using varying δ^{13}C-enrichment steps and trophic levels to determine the range of possible solutions and sensitivity to model parameters (Brittain et al. 2009). Mixing models were based on six potential sources for

Sapelo Island and the three sources for Clayhole Swamp identified using MRPP. A matrix of nine potential models was run in *Isosource* for each species based on three different trophic levels (ranging from 2 to 4, depending on the species) varying 0.5 steps based on the estimated trophic position (λ) using the equation:

$\lambda = (\delta N_b - \delta N_s)/ \delta N_h$, where λ is the estimated number of trophic steps between the birds and their food resources, δN_b is the average $\delta^{15}N$ value of the bird species, δN_s is the average $\delta^{15}N$ value of the primary food sources and δN_h is the average difference in $\delta^{15}N$ between known herbivores and plants among all habitats. All isotopic values of potential sources in mixing models for each species were enriched by λ rounded off to the nearest half-step, plus or minus two other 0.5 trophic steps, to compare a range of potential solutions. Estimated ^{13}C-enrichment of primary production sources for each trophic step before feathers (i.e., plants and invertebrates) was the average difference between known herbivores and source plants among all habitats in this study (+ 1.3‰, n = 31 invertebrates and 61 plants). Production sources were thus ^{13}C-enriched + 1.3‰ for each trophic level through invertebrates, and the final trophic step to the feathers was either + 2.5‰, + 3.5‰ or + 4.5‰ to account for variable isotopic enrichment with insectivory (Pearson et al. 2003). For example, a species estimated at 2.5 trophic levels would have been ^{13}C-enriched by + 1.3‰ for the first 1.5 trophic steps and either 2.5‰, 3.5‰ or 4.5‰ for the final trophic step. Since there is less variation in trophic ^{15}N-enrichment to feathers than ^{13}C (Pearson et al. 2003), ^{15}N-enrichment was not varied from model to model. ^{15}N was similarly increased by the average difference between known herbivores and source plants among all habitats in this study for each trophic step before the bird diet (+ 2.26‰, n= 31 invertebrates and 61 plants) and + 3.3‰ for the last trophic step to the feathers (Pearson et al. 2003).

The standard deviations of all sources within each model for each species were averaged (source SD), as well as the standard deviations of the mean results for each source across all models (model SD) as measures of internal *Isosource* variability. Source SD and model SD were compared using *t*-tests, assuming non-equal variances, to assess the greater source of variability. External *Isosource* variability was measured as the average standard deviations due to changes in trophic level and isotopic enrichment, which were similarly tested for differences and compared to the internal *Isosource* variability.

The percent contribution of potential invertebrate and plant prey sources that may have been eaten directly by the birds were also modeled for all species except Eastern Screech Owl (no vertebrates were sampled) in *Isosource*. Since these models represent materials consumed directly by the birds, sources were isotopically enriched by one trophic step only (Brittain et al. 2009). *Isosource* sensitivity anlaysis of prey partitioning ran nine models for each species with feather ^{13}C-enriched by either + 2.5‰, + 3.5‰ or + 4.5‰, and ^{15}N-enriched at the same three rates, except for the saltmarsh species (Clapper Rail and Marsh Wren) which were ^{13}C-enriched by + 0.5‰, + 1.0‰ or + 2.0‰ due to lack of successful models using the previously assumed enrichment levels. Primary production model results and known feeding habits were used to determine which habitats (saltmarsh or the terrestrial habitats they were captured in) that invertebrate sources should be partitioned for each species (Table 5). Primary production models generally showed the relative contribution of saltmarsh vs. terrestrial plants to avian food webs, and models showing a consistent 20% or more contribution from any particular habitat source (saltmarsh vs. terrestrial vegetation) were included in prey source models. Internal and external prey model variabilities were analyzed the same as primary production.

RESULTS

Plant and invertebrate isotopic values

Multi-Response Permutation Procedures revealed six distinct producer sources from the four habitats on Sapelo Island and three producer sources in the tidal forest ($P < 0.001$ and $P < 0.018$, respectively; Table 1). Sapelo Island primary production sources were C_3 berries, C_3 leaves, C_3 saltmarsh vegetation, C_4 grasses, C_4 saltmarsh vegetation and CAM plants. Tidal forest primary production sources were bald cypress, herbaceous vegetation and other species. Differences between primary production sources were caused not only by ^{13}C values due to photosynthetic pathway fractionation, but also ^{15}N values due to fractionation differences between hydrologic regimes (anaerobic vs. aerobic soils). Average isotopic values and standard deviations for each plant species in each habitat can be found in Appendix 1.

Saltmarsh and tidal forest invertebrates had distinct guilds within their respective habitats: carnivores, parasites and omnivores (CPO), detritivores (D), and herbivores and fungivores (HF; $P < 0.0005$; Table 2). However, terrestrial habitats on Sapelo Island had some overlap between guilds: oak and pine forest combined CPO and HF ($P < 0.0005$), while shrub and pine forest combined D, ($P < 0.013$) and shrub CPO and HF were distinct ($P < 0.0005$). Average isotopic values and standard deviations for each invertebrate family in each habitat can be found in Appendix 2.

Bird isotopic values by habitat

Brown-headed Nuthatch isotopes were different between pine forest and shrub ($P = 0.017$; Table 3 and Figure 2), and Carolina Wren and Northern Parula isotopes on Sapelo Island were different than those in tidal forests ($P < 0.0005$; Figures 2 & 3). There were no isotopic differences between habitats for Eastern Screech Owls, Painted Buntings, White-eyed Vireos and Yellow-throated Warblers.

Feather isotopic values by capture day, feather age (known vs unknown origin) and sex

There were no isotopic differences between first capture and recapture of Brown-headed Nuthatch or Northern Parula. The only differences between feathers of known and unknown origins, and between sexes, were due to differences in either the age of birds (young of year vs. adult) or geographic location (tidal forest vs. Sapelo Island habitats; Appendix 3).

Bird feather isotopic values by age

Young of year Brown-headed Nuthatch and Yellow-throated Warbler isotopes were significantly different than after hatch year and second year birds ($P < 0.025$ and $P < 0.0005$, respectively; Table 4). Young of year White-eyed Vireos were only different than after hatch year birds ($P < 0.0005$). Isotopic differences between ages of all three species were from increased δ^{15}N values in the young of year birds. Carolina Wrens, Eastern Screech Owls, Northern Parula and Painted Buntings had no isotopic differences among age classes.

Bird trophic position

The lowest estimated trophic position (λ) on Sapelo Island was for Northern Parula in shrub habitat (2.4), and the highest trophic position was occupied by Eastern Screech Owl in pine forest (4.3; Table 5 and Figure 2). Most terrestrial bird species had similar isotope signatures, but Painted Buntings were elevated in δ^{13}C (-14.87‰) similar to Clapper Rails (-14.04‰) and Marsh Wrens (-14.23‰). Eastern Screech Owls (7.4‰), Carolina Wrens (7.2‰) and Red-bellied Woodpeckers (6.8‰) had more positive δ^{15}N than other terrestrial bird species. In tidal forest habitat, Carolina Wrens had the highest trophic level (1.9; Figure 3). Carolina Wrens and Northern Parula were strongly enriched by ~6‰ in both δ^{13}C and δ^{15}N relative to tidal forest vegetation.

Primary production source mixing models

No primary production source models were successfully run for either Carolina Wrens or Northern Parula in tidal forest habitat.

Within the saltmarsh, C_4 saltmarsh vegetation (*Spartina alterniflora*) had the highest primary production source means for Clapper Rails, ranging from 34.8% ± 5.9 to 64.2% ± 1.9 (Figure 4). However, C_3 saltmarsh vegetation from the high saltmarsh zone had the highest mean results for Marsh Wrens (34.1% ± 9.0 to 61.2% ± 3.6). The proportion of C_4 saltmarsh vegetation decreased with increasing trophic levels and ^{13}C-enrichment for both species, while C_3 saltmarsh vegetation increased with enrichment and changed little due to trophic level.

C_3 leaves consistently contributed the most primary production source to the foodwebs of Eastern Screech Owls, White-eyed Vireos of all ages, Red-bellied Woodpeckers, Brown-headed Nuthatches of all ages and in both habitats, Carolina Wrens on Sapelo Island, and Northern Parula on Sapelo Island and Yellow-throated Warblers of all ages (Figure 4). The proportion of C_3 leaves for each species increased with both trophic level and ^{13}C-enrichment in both habitats and ages. C_3 saltmarsh vegetation proportionally decreased only with trophic level, while C_3 berries decreased with ^{13}C-enrichment.

Painted Bunting primary production source models were the obvious exception to the overall trend on Sapelo Island with few differences between each source across all models (Figure 4). The C_4 saltmarsh source was more variable than other Painted Bunting sources, but also had the highest mean (10.6% ± 5.7 to 40.6% ± 5.0). C_4 grasses had the next highest mean Painted Bunting source partition (10.2% ± 6.7 to 25.8% ± 14.4). The relative contribution of C_4 saltmarsh vegetation decreased with increasing trophic level and ^{13}C-enrichment. C_4 grass and CAM plant proportions decreased with enrichment and increased with trophic level, whereas all three C_3 sources increased with enrichment and trophic level.

Internal *Isosource* variation analysis showed that source SD results across all models were higher than individual model SD results (t = -4.40, df = 31, P < 0.0005). There was no difference between standard deviations due to assumed trophic levels and ^{13}C-enrichment rates (t

= -0.41, df = 29, *P* = 0.688). Both internal variability sources (source SD and model SD) were lower than the external sources due to trophic levels or ^{13}C-enrichment (*P* < 0.0005).

Invertebrate source mixing models

In tidal forests, the highest mean prey source partitions for Carolina Wrens were from (33.5% ± 3.7 to 88.7% ± 0.8; Figure 5). For Northern Parula, however, while CPO from oak and pine forests were greatest on Sapelo Island, detritivores had the greatest proportions of Northern Parula prey sources in tidal forest (20.5% ± 4.7 to 85.0% ± 4.6). Both species showed more use of detritivores with increased ^{15}N-enrichment in tidal forests.

In saltmarsh habitat on Sapelo Island, Clapper Rail prey source partitioning was highly variable among the three saltmarsh guilds (Figure 5). Marsh Wren prey source models showed CPO had the highest results (48.7% ± 3.7 to 82.6% ± 3.6). Models for both species increased the proportion of detritivores with both $\delta^{13}C$ and $\delta^{15}N$ increases. The percent of HF increased with ^{15}N-enrichment, but decreased with ^{13}C-enrichment, whereas the percent of CPO decreased with ^{13}N-enrichment.

On Sapelo Island terrestrial habitats, CPO had the highest mean prey source partitions for Red-bellied Woodpeckers, White-eyed Vireos of all ages, Carolina Wrens, Brown-headed Nuthatches of all ages in both shrub and pine forest habitats, Northern Parula and Yellow-throated Warblers (Figure 5). Prey source model results were highly variable for all species, with few clear trends (species-specific) in response to isotopic trophic enrichment. However, the proportion of CPO in most species decreased with ^{15}N-enrichment.

Painted Bunting prey source models showed that saltmarsh HF and C_4 grasses had the largest partitions (18.9% ± 11.2 to 31.3% ± 17.5 saltmarsh HF and 9.0% ± 5.8 to 36.3% ± 4.7 C_4 grasses; Figure 5). It should be noted that no models using only terrestrial sources of invertebrates and vegetation for Painted Buntings were successful. Four Painted Bunting sources (detritivores in shrub and pine forest, berries, and shrub CPO and HF) showed no response to ^{15}N-enrichment but increased slightly with ^{13}C-enrichment. C_4 grass proportionately decreased with ^{13}C-enrichment and increased with ^{15}N-enrichment, whereas HF and CPO from saltmarshes decreased with ^{15}N-enrichment and responded little to ^{13}C.

Internal *Isosource* variability analysis showed model SD results were higher than individual source SD results (t = -5.38, df = 18, $P < 0.0005$). There was no difference in standard deviations of external variability due to trophic levels and ^{13}C-enrichment (t = -0.54, df = 23, P = 0.597). Both internal *Isosource* variability sources were lower than those due to trophic levels or ^{13}C-enrichment ($P < 0.0005$).

Discussion

Bird isotopic signatures

Isotopic differences between fresh feathers of known origin and old feathers of unknown origin for Brown-headed Nuthatches, White-eyed Vireos and Yellow-throated Warblers corresponded with differences in ages since young of year birds overwhelmingly supplied the fresh feathers. The similarity of old and fresh feathers for all other species showed that it was safe to combine them for analyses of the population, but the different ages needed to be analyzed separately.

Three species (Brown-headed Nuthatch, White-eyed Vireo and Yellow-throated Warbler) showed isotopic differences between the young of year and adult birds despite being non-migratory (Barlow 1980, Hall 1996, Withgott and Smith 1998), primarily due to δ^{15}N (Table 4). Higher δ^{15}N values among young of year birds indicate a potential diet switch from higher trophic positions for young of year to lower trophic positions in adults of these species as seen in Tufted Puffins (*Fratercula cirrhata*; Williams et al. 2008). The difference between young of year and adult trophic positions for insectivorous White-eyed Vireos and Yellow-throated Warblers may be due to a diet switch with timing of the molt since adults grow retrices later than young of year (Pyle 1997).

Since λ was based on average $\delta^{15}N$ values for all vegetation within the habitat, differences between λ and the trophic level necessary to model the results are likely due to differences in the relative proportion of various source pathways, requiring information on the exact proportion of food sources in order to estimate trophic positions using stable isotopes. High trophic positions estimated by λ values for an omnivorous species, such as Brown-headed Nuthatch, may be due to the prevalence of young of year within the data, which would have been fed exclusively invertebrates during the period of feather growth (Norris 1958). Similarly, the high trophic positions estimated for omnivorous adult Painted Buntings and Red-bellied Woodpeckers may be due to more reliance on invertebrates during the molting period (Lowther et al. 1999, Shackelford et al. 2000). A more likely reason for the difference between estimated and modeled trophic positions for Painted Buntings is because a large portion of their diet came from a unique source, the saltmarsh, which inflated their perceived $\delta^{15}N$ values relative to the habitat they occupied. We also cannot rule out the possibility that any of these species may fractionate $\delta^{15}N$ differently than other species, despite Pearson et alia's evidence of little variation among Yellow-rumped Warblers (2006). For example, Birchall et al. (2005) found that aquatic carnivores showed less ^{15}N-enrichment than terrestrial carnviores, and Sears et al. (2009) found that Rhinoceros Auklet chicks (*Cerorhinca monocerata*) were depleted in ^{15}N when they were nutritionally stressed by lack of food or fast growth. However, the results from Sears et al. indicate an expected decrease in $\delta^{15}N$ among young of year birds relative to adults of the same species, but our results clearly showed that young of year had increased $\delta^{15}N$ relative to the adults. Either the ^{15}N depletion was minimal among the young of year birds, the young of year were being fed from a much higher trophic level than adults, or the adults were more nutritionally stressed during their time of feather growth in late summer/early fall (Pyle 1997).

Primary production source partitions

The trophic steps assumed in the primary production source models and feather ^{13}C-enrichment not only created the same variability in source partitions but were also responsible for more variability in the models than the internal *Isosource* variability (Figures 4 & 5). Models assuming both high trophic levels and ^{13}C-enrichment increased the proportion of C_3 leaves in avian diets, but models with low trophic levels switched the results to more reliance on C_3 saltmarsh vegetation. Similarly, dependence on berries decreased with ^{13}C-enrichment. These results demonstrate the importance of accurately determining both trophic position and rate of isotopic enrichment when partitioning isotope sources.

The lack of successful *Isosource* mixing models for Carolina Wrens and Northern Parula in the tidal forests of the Clayhole Swamp indicates that minimal isotopic differences between C_3 sources in one habitat may not be enough to partition the sources, as Bearhop and others (2004) suggested. Sapelo Island has a diverse range of photosynthetic pathways in both aerobic and anaerobic soil conditions that led to distinct isotopic signals, but tidal forest only included C_3 vegetation in anoxic soils.

Both Carolina Wrens and Northern Parula were isotopically increased in $\delta^{13}C$ by approximately 6‰ over the vegetation in tidal forest, which is far higher than expected. Birds in tidal forests may fractionate carbon isotopes differently than the same species in other habitats, they may be feeding somewhere other than the tidal forest, or the sampling strategy may have failed to find an important source of productivity within the tidal forest. Exploratory analysis of total suspended solids and chlorophyll-*a* in tidal water and surface soils showed no differences in

$\delta^{13}C$ between these sources and sampled vegetation, implicating differential carbon fractionation in tidal forest.

Invertebrate source partitions

The different levels of assumed feather ^{13}C and ^{15}N-enrichment in invertebrate mixing models equally caused the highest changes in source partitioning (Figures 4 & 5). On Sapelo Island the birds showed many species-specific effects of isotopic enrichment. However, the overwhelming trend was for models to show decreasing dependence on CPO, and a corresponding increase in HF and/or detritivores, as ^{15}N values became more positive. In tidal forests, the variability due to enrichment appeared to have similar patterns with both Carolina Wren and Northern Parula by shifting from CPO to detritivores with increasing ^{15}N values.

Invertebrate sources for both saltmarsh species, Clapper Rail and Marsh Wren, could not be partitioned successfully at the expected 2.5‰ to 4.5‰ ^{13}C-enrichment levels and were only successful with 0.5‰ to 1.5‰ enrichment. The lack of consistency between saltmarsh and other species suggests that trophic ^{13}C-enrichment steps may differ in the harsh abiotic conditions of the saltmarsh, similar to the different ^{15}N-enrichment rates found by Birchall et al. (2005).

CONCLUSIONS

Tracing food webs using stable isotopes in small geographic areas is not only possible in regions where there are diverse photosynthetic pathways, as already known (Hobson 1999, Kelly 2000), but also different hydrologic conditions (anaerobic vs. aerobic) that create the necessary isotopic differences for source partitioning. However, even habitats with limited differences in primary production sources may still have prey items with distinctive isotopic signatures. Since the species' trophic level and isotopic enrichment contribute the most variability to *Isosource* results, it is imperative that researchers have a close approximation of these parameters to accurately partition sources to the organisms of interest, or conduct similar sensitivity analyses and average the results to determine the best estimate. While *Isosource* models show that the trophic enrichment of both ^{13}C and ^{15}N in feathers can alter partition results, $\delta^{15}N$ expresses a narrower range of feather isotopic enrichment than does $\delta^{13}C$ and should be less problematical (Pearson et al. 2003), but researchers may need to control for differences in ^{15}N-enrichment between stressed or growing individuals (Sears et al. 2009). More research on species specific trophic increases of ^{13}C and ^{15}N in feathers, as well as ^{34}S and D, clearly needs to be done. Researchers should account for variation of ^{13}C and ^{15}N-enrichment in trophic studies either through sensitivity analysis or species enrichment experiments.

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TABLE 1. Isotopic signatures of primary production sources in coastal Georgia.

Location	Source	N	$\delta^{13}C$	$\delta^{15}N$
Oak & pine forest and shrub	C_3 berries	24	-27.51 ±0.09	-2.2 ±0.1
	C_3 leaves	66	-29.74 ±0.03	-1.5 ±0.0
	CAM plants	6	-16.08 ±0.14	-5.9 ±0.1
	C_4 grasses	5	-13.46 ±0.07	-2.4 ±0.2
Saltmarsh	C_3 saltmarsh	16	-26.84 ±0.11	1.8 ±0.2
	C_4 saltmarsh	8	-13.92 ±0.12	5.6 ±0.2
Tidal forest	Cypress	6	-30.56 ±0.28	3.0 ±0.3
	Herbs	9	-33.59 ±0.12	2.6 ±0.1
	Other	21	-31.91 ±0.04	1.0 ±0.1

Mean $\delta^{13}C$ (in ‰) and $\delta^{15}N$ (in ‰) ± 1 SE of pooled isotopic results. See Appendix 1 for individual species results. All groups within each habitat were significantly different between each other using Multi-Response Permutation Procedures ($\alpha = 0.05$).

TABLE 2. Isotopic signatures of invertebrate prey sources in coastal Georiga, grouped by feeding guild.

	Invertebrate Feeding Guild								
	Herbivores/Fungivores			Detritivores			Carnivores/Parasites/Omnivores		
Habitat	N	$\delta^{13}C$	$\delta^{15}N$	N	$\delta^{13}C$	$\delta^{15}N$	N	$\delta^{13}C$	$\delta^{15}N$
saltmarsh	33	-14.02 ±0.20	8.1 ±0.3	6	-16.32 ±0.50	4.4 ±0.4	13	-14.76 ±0.69	9.8 ±0.8
shrub	70	-24.40 ±0.46	1.8 ±0.2				44	-23.43 ±0.37	4.8 ±0.4
oak forest				9	-27.70 ±0.18	-1.4 ±0.2			
oak & pine forest	48	-26.27 ±0.51	0.8 ±0.3				51	-26.21 ±0.21	3.6 ±0.3
shrub & pine forest				17	-26.54 ±0.25	0.0 ±0.7			
tidal forest	55	-29.18 ±0.31	3.2 ±0.3	11	-27.26 ±0.34	3.7 ±0.6	44	-27.60 ±0.21	5.3 ±0.2
Contributing taxonomy	acarina, alleculide, alydidae, aphididae, buprestidae, cercopidae, chrysomelidae, cicadellidae, ciidae, cixiidae, curculionidae, delphacidae,			bibioniidae, blattaria, culicidae, diplopoda, ocypodidae, psocidae, tipulidae			araneae, braconidae, cleridae, coccinellidae, dolichopodidae, eurytomidae, formicidae, mantidae, reduviidae, sphecidae, tiphiidae		

	elateridae, flatidae, lepidoptera, littorinidae, lygaeidae, miridae, mordellidae, ortheziidae, orthoptera, pentatomidae, phalacridae, tephritidae, thysanoptera

Mean $\delta^{13}C$ (in ‰) and $\delta^{15}N$ (in ‰) ± 1 SE of pooled isotopic results. See Appendix 2 for taxonomic family results. All groups within each habitat were significantly different between each other using Multi-Response Permutation Procedures ($\alpha = 0.05$).

TABLE 3. Isotopic signatures of avian species in five habitats of coastal Georgia.

Habitat	Species	λ	N	$\delta^{13}C$	$\delta^{15}N$
Tidal forest	**Carolina Wren***	**1.9**	**13**	**-24.35 ±0.21**	**7.6 ±0.3**
	Northern Parula†	**1.8**	**23**	**-23.95 ±0.12**	**7.3 ±0.4**
Saltmarsh	Clapper Rail	2.6	4	-14.04 ±0.78	10.6 ±0.6
	Marsh Wren	3.6	18	-14.23 ±0.89	12.9 ±0.3
Shrub	Eastern Screech Owl	4.2	4	-21.84 ±0.37	6.9 ±0.5
	White-eyed Vireo	3.2	33	-23.28 ±0.17	6.2 ±0.6
	Brown-headed Nuthatch‡	**3.2**	**5**	**-22.76 ±0.37**	**4.9 ±0.4**
	Carolina Wren*	**3.6**	**13**	**-21.46 ±0.42**	**7.2 ±0.2**
	Northern Parula	2.4	3	-23.58 ±0.80	4.5 ±0.4
	Yellow-throated Warbler	2.6	6	-23.67 ±0.21	4.8 ±0.5
	Painted Bunting	3.3	27	-15.02 ±0.79	6.4 ±0.6
Oak forest	Eastern Screech Owl	4.2	13	-22.38 ±0.15	7.2 ±0.2
	Red-bellied Woodpecker	3.3	1	-23.58 ±0.06	5.2 ±0.2
	White-eyed Vireo	3.5	6	-23.70 ±0.31	5.6 ±0.3

	Carolina Wren*	**4.2**	**6**	**-22.68 ±0.29**	**7.2 ±0.5**
	Northern Parula†	**3.3**	**62**	**-23.76 ±0.07**	**5.4 ±0.3**
	Yellow-throated Warbler	3.3	21	-23.19 ±0.13	5.3 ±0.3
	Painted Bunting	4.0	4	-16.67 ±2.86	7.0 ±0.3
Pine forest	Eastern Screech Owl	4.3	11	-22.76 ±0.32	7.8 ±0.2
	Red-bellied Woodpecker	3.9	12	-22.30 ±0.13	6.8 ±0.2
	White-eyed Vireo	3.2	7	-24.56 ±0.27	5.3 ±0.3
	Brown-headed Nuthatch‡	**3.2**	**51**	**-22.20 ±0.09**	**5.2 ±0.1**
	Carolina Wren*	**4.0**	**2**	**-22.70 ±0.24**	**7.1 ±0.4**
	Northern Parula	3.4	2	-23.87 ±0.16	5.8 ±0.2
	Yellow-throated Warbler	2.9	3	-23.16 ±0.21	5.1 ±0.8
	Painted Bunting	4.1	9	-13.62 ±1.24	7.3 ±0.7

* = Carolina Wren isotopic results are different between tidal forest and Sapelo Island habitats.

† = Northern Parula isotopic results are different between tidal and oak forests.

‡ = Brown-headed Nuthatch isotopic results are different between pine forest and shrub habitat.

Analyses based on Multi Response Permutation Procedures, corrected using sequential Bonferroni methods ($\alpha = 0.05$).

Mean $\delta^{13}C$ (in ‰) and $\delta^{15}N$ (in ‰) ± 1 SE of feather results. See text for scientific names of bird species. Standard errors have been additively propagated with the instrument error. λ = estimated trophic position.

TABLE 4. Isotopic signature of avian species by age in coastal Georgia.

Age	Species	N	$\delta^{13}C$	$\delta^{15}N$
Hatch year	Painted Bunting	2	-16.14 ±3.85	6.6 ±3.0
After hatch year	Clapper Rail	3	-14.37 ±1.01	10.3 ±0.7
	Eastern Screech Owl	18	-22.36 ±0.15	7.4 ±0.2
	Red-bellied Woodpecker	5	-22.54 ±0.29	6.2 ±0.3
	White-eyed Vireo*	**23**	**-23.76 ±0.23**	**5.5 ±0.2**
	Brown-headed Nuthatch†	**22**	**-22.11 ±0.17**	**4.9 ±0.2**
	Carolina Wren	14	-22.49 ±0.53	7.3 ±0.3
	Marsh Wren	9	-15.18 ±1.43	12.5 ±0.6
	Northern Parula	68	-23.90 ±0.07	5.9 ±0.3
	Yellow-throated Warbler†	**11**	**-23.27 ±0.15**	**4.4 ±0.3**
	Painted Bunting	28	-15.24 ±0.80	6.9 ±0.5
Young of year	CLRA	1	-13.06 ±0.06	11.6 ±0.2
	Eastern Screech Owl	1	-23.04 ±0.06	7.4 ±0.2
	White-eyed Vireo*	**22**	**-23.28 ±0.19**	**6.5 ±0.2**

	Brown-headed Nuthatch†	**22**	**-22.33 ±0.09**	**5.6 ±0.2**
	Carolina Wren	2	-22.83 ±0.04	6.2 ±0.8
	Yellow-throated Warbler†	**12**	**-22.92 ±0.10**	**6.1 ±0.3**
Second year	Eastern Screech Owl	9	-22.56 ±0.40	7.3 ±0.4
	Red-bellied Woodpecker	1	-23.36 ±0.06	5.6 ±0.2
	White-eyed Vireo	1	-23.60 ±0.06	6.4 ±0.2
	Brown-headed Nuthatch†	**12**	**-22.16 ±0.23**	**4.7 ±0.1**
	Carolina Wren	18	-23.13 ±0.35	7.5 ±0.2
	Marsh Wren	9	-13.28 ±1.07	13.2 ±0.3
	Northern Parula	19	-23.51 ±0.14	5.7 ±0.3
	Yellow-throated Warbler†	**7**	**-23.76 ±0.23**	**5.0 ±0.3**
	Painted Bunting	10	-13.59 ±1.21	6.0 ±0.8
After second year	Red-bellied Woodpecker	7	-22.16 ±0.13	7.3 ±0.1
	Northern Parula	3	-23.49 ±0.72	4.2 ±2.9

* = After hatch year White-eyed Vireos different than young of year birds.

† = After hatch year and second year Brown-headed Nuthatches and Yellow-throated Warblers different than young of year birds.

Analyses based on Multi Response Permutation Procedures, corrected using sequential Bonferroni methods ($\alpha = 0.05$).

Mean $\delta^{13}C$ (in ‰) and $\delta^{15}N$ (in ‰) ± 1 SE of feather results. Hatch Year birds were in their first breeding season at time of capture. Young of year birds were hatched during the breeding season of capture. Standard errors have been additively propagated with the instrument error.

TABLE 5. Potential prey sources modeled for each species.

Species	Habitat/Age	Prey	Sources
Clapper Rail	Saltmarsh	CPO, D and HF	Oney 1951, Meanley 1985
Red-bellied Woodpecker	Pine forest	Oak & pine CPO & HF	Beal 1911
		Shrub & pine D	
		Pine vegetation	
		Berries	
White-eyed Vireo	Sapelo Island, young of year	Oak & pine CPO & HF	Beal et al. 1916, Chapin 1925,
	and after hatch year	Berries	Nolan and Woolridge 1962
		Shrub CPO & HF	
		Shrub & pine D	
Marsh Wren	Saltmarsh	CPO, D and HF	Kale 1964
Carolina Wren	Sapelo Island	Oak & pine CPO & HF	Beal et al. 1916
		Berries	
		Shrub CPO & HF	
		Shrub & pine D	

Carolina Wren	Tidal forest	CPO, D and HF	Beal et al. 1916
Brown-headed Nuthatch	Pine forest, young of year and after hatch year	Oak & pine CPO & HF Shrub & pine D Pine vegetation	Norris 1958
Northern Parula	Sapelo Island	Oak & pine CPO & HF Oak D Shrub CPO & HF Shrub & pine D	Howell 1932, Stevenson and Anderson 1984
Northern Parula	Tidal forest	CPO, D and HF	Howell 1932, Stevenson and Anderson 1984
Yellow-throated Warbler	Sapelo Island, young of year and after hatch year	Oak & pine CPO & HF Oak D Shrub CPO & HF Shrub & pine D	Howell 1932, Stevenson and Anderson 1984, Hall 1996
Painted Bunting	Sapelo Island	Saltmarsh CPO & HF Shrub CPO, D & HF	Howell 1932

Berries & C_4 terrestrial grasses

FIG. 1. Map of study area on Sapelo Island, McIntosh County, Georgia and location of bird banding sites in saltmarsh, maritime scrub-shrub, maritime broadleaf evergreen forest and maritime narrowleaf evergreen forest.

FIG. 2. Isoscape of $\delta^{13}C$ and $\delta^{15}N$ values for plants, invertebrate guilds and birds sampled on Sapelo Island, Georgia in 2006-2007. CLRA = Clapper Rail, EASO = Eastern Screech Owl, RBWO = Red-bellied Woodpecker, WEVI = White-eyed Vireo, BHNU = Brown-headed Nuthatch, CARW = Carolina Wren, MAWR = Marsh Wren, NOPA = Northern Parula, YTWA = Yellow-throated Warbler and PABU = Painted Bunting. “opC” = carnivores, parasites and omnivores from oak and pine forests, “oD” = detritivores from oak forest, “opH” = herbivores and fungivores from oak and pine forests, “shC” = carnivores, parasites and omnivores from shrub habitat, “shpD” = detritivores from shrub and pine forest, “shH” = herbivores and fungivores from shrub habitat, “saC” = carnivores, parasites and omnivores from saltmarsh, “saD” = detritivores from saltmarsh, and “saH” = herbivores and fungivores from saltmarsh.

FIG. 3. Isoscape of $\delta^{13}C$ and $\delta^{15}N$ values for plants, invertebrate guilds and birds sampled in Clayhole Swamp, Georgia in 2006-2007. CARW = Carolina Wren and NOPA = Northern Parula. “C” = carnivores, parasites and omnivores, “D” = detritivores, and “H” = herbivores and fungivores from tidal forests.

FIG. 4. Mean percent food coming from major sources of primary production for birds on Sapelo Island, Georgia based on *Isosource* mixing models with different assumed trophic steps and ^{13}C-enrichment. Trophic steps of each species ranged from 2.0 to 4.0 steps at 0.5 intervals, and feather ^{13}C-enrichment was either + 2.5‰, + 3.5‰ or + 4.5‰ for a total of nine potential models

per species. Each line represents the results from one model. CLRA = Clapper Rail, EASO = Eastern Screech Owl, RBWO = Red-bellied Woodpecker, WEVI = White-eyed Vireo, BHNU = Brown-headed Nuthatch, CARW = Carolina Wren, MAWR = Marsh Wren, NOPA = Northern Parula, YTWA = Yellow-throated Warbler and PABU = Painted Bunting. Sources: “C3B” = C_3 berries, “C3L” = C_3 leaves, “C3S” = C_3 saltmarsh vegetation, “C4G” = C_4 grasses, “C4S” = *Spartina alterniflora*, and “CAM” = CAM plants. “AHY” = after hatch year birds and “YOY” = young of year birds.

FIG. 5. Mean percent of food coming directly from invertebrate and plant sources for birds in coastal Georgia based on *Isosource* mixing models with feather ^{13}C-enrichment at + 2.5‰, + 3.5‰ or + 4.5‰, and feather ^{15}N-enrichment at + 2.5‰, + 3.5‰ or + 4.5‰ for a total of nine potential models per species. Each line represents the results from one model. CLRA = Clapper Rail, RBWO = Red-bellied Woodpecker, WEVI = White-eyed Vireo, BHNU = Brown-headed Nuthatch, CARW = Carolina Wren, MAWR = Marsh Wren, NOPA = Northern Parula, YTWA = Yellow-throated Warbler and PABU = Painted Bunting. Sources are: “CPO” = carnivores, parasites and omnivores, “Det” = detritivores, “HF” = herbivores and fungivores, “op” = coming from oak and pine forests, “o” = coming from oak forest only, “sh” = coming from shrub only, “shp” = coming from shrub and pine forest, and “sa” = coming from saltmarsh. “C3B” = C_3 berries, “C4G” = C_4 grasses and “pine” = pine vegetation. “AHY” = after hatch year birds and “YOY” = young of year birds.

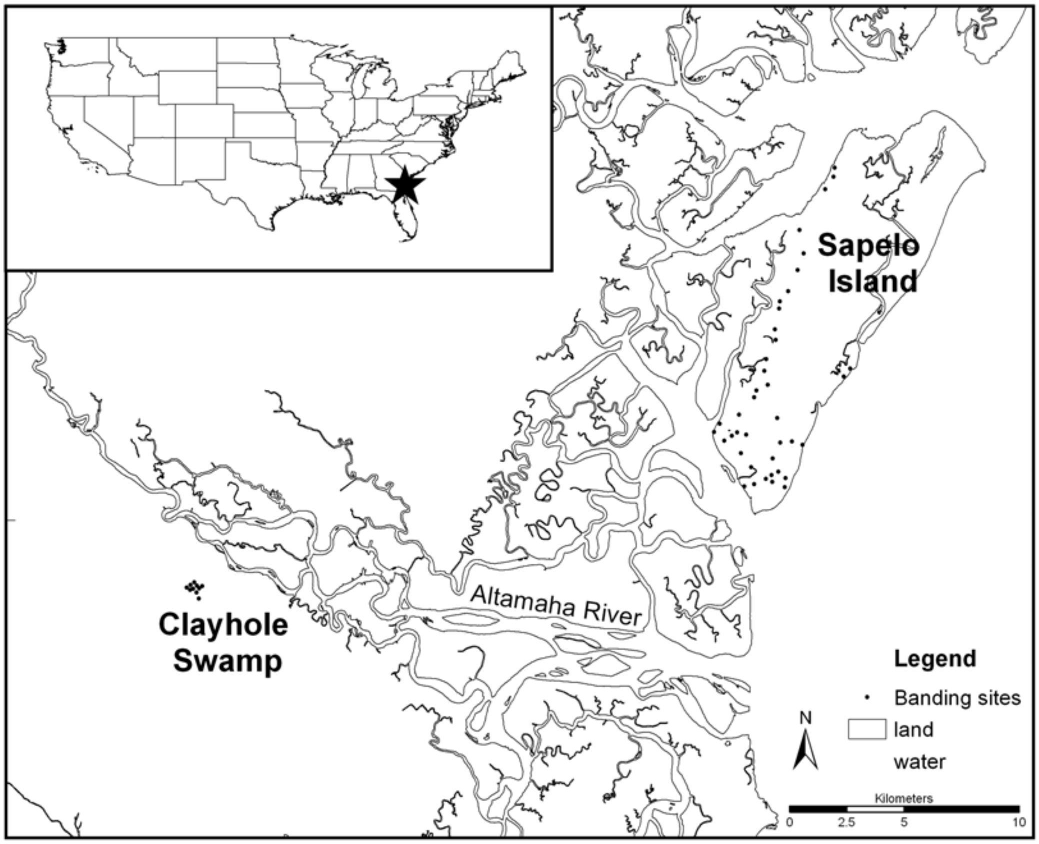
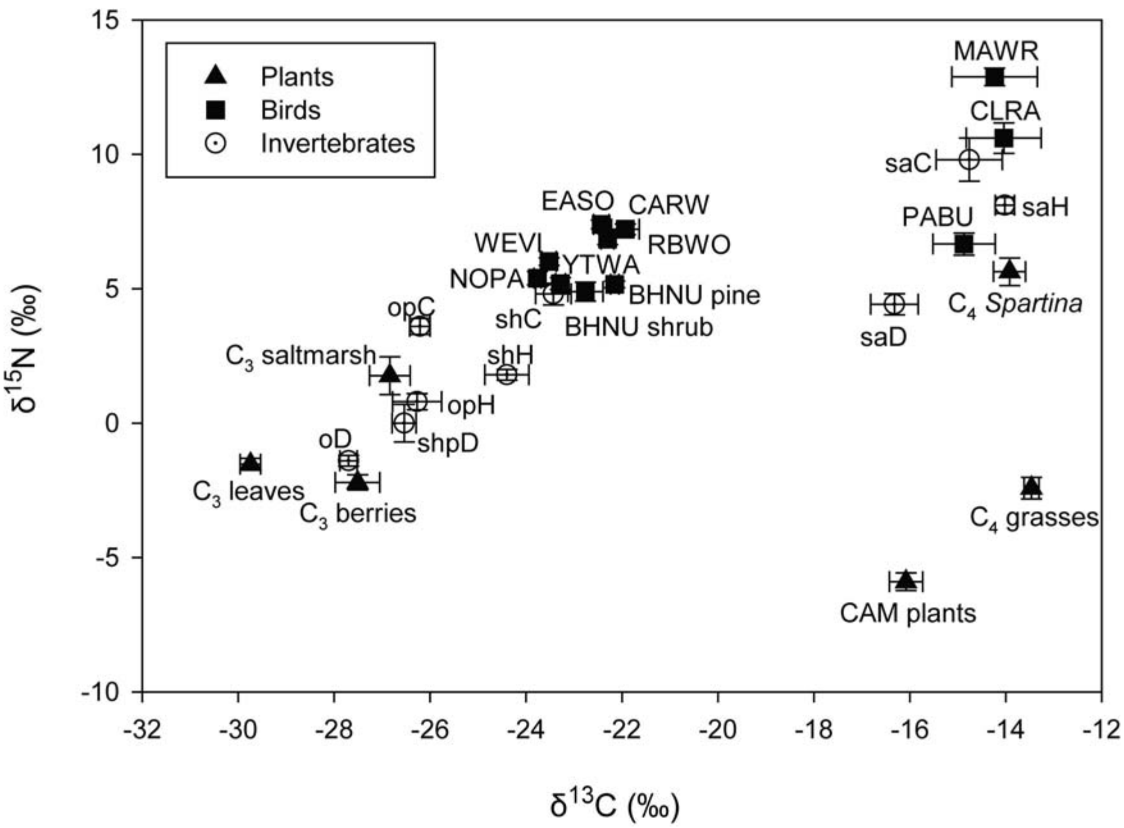
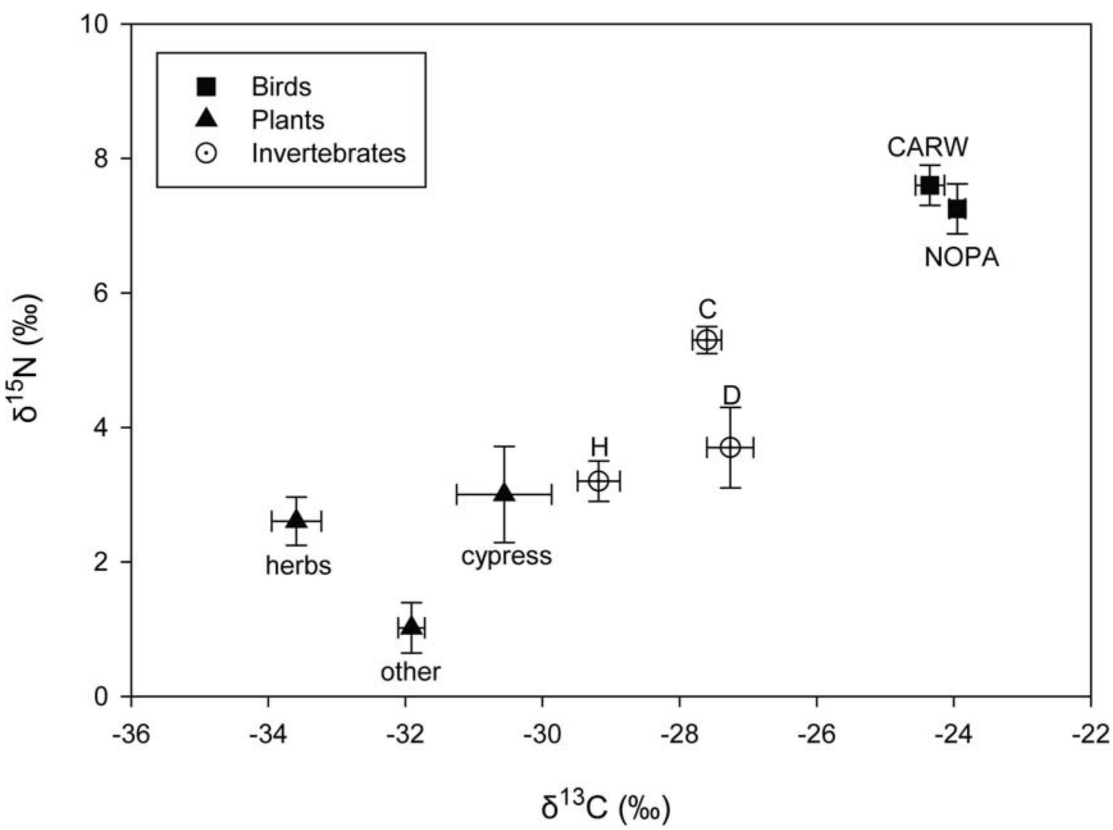

Sapelo Island
Clayhole Swamp
Altamaha River
Legend
Banding sites
land
water
N
Kilometers
0
2.5
5
10

Figure 1.



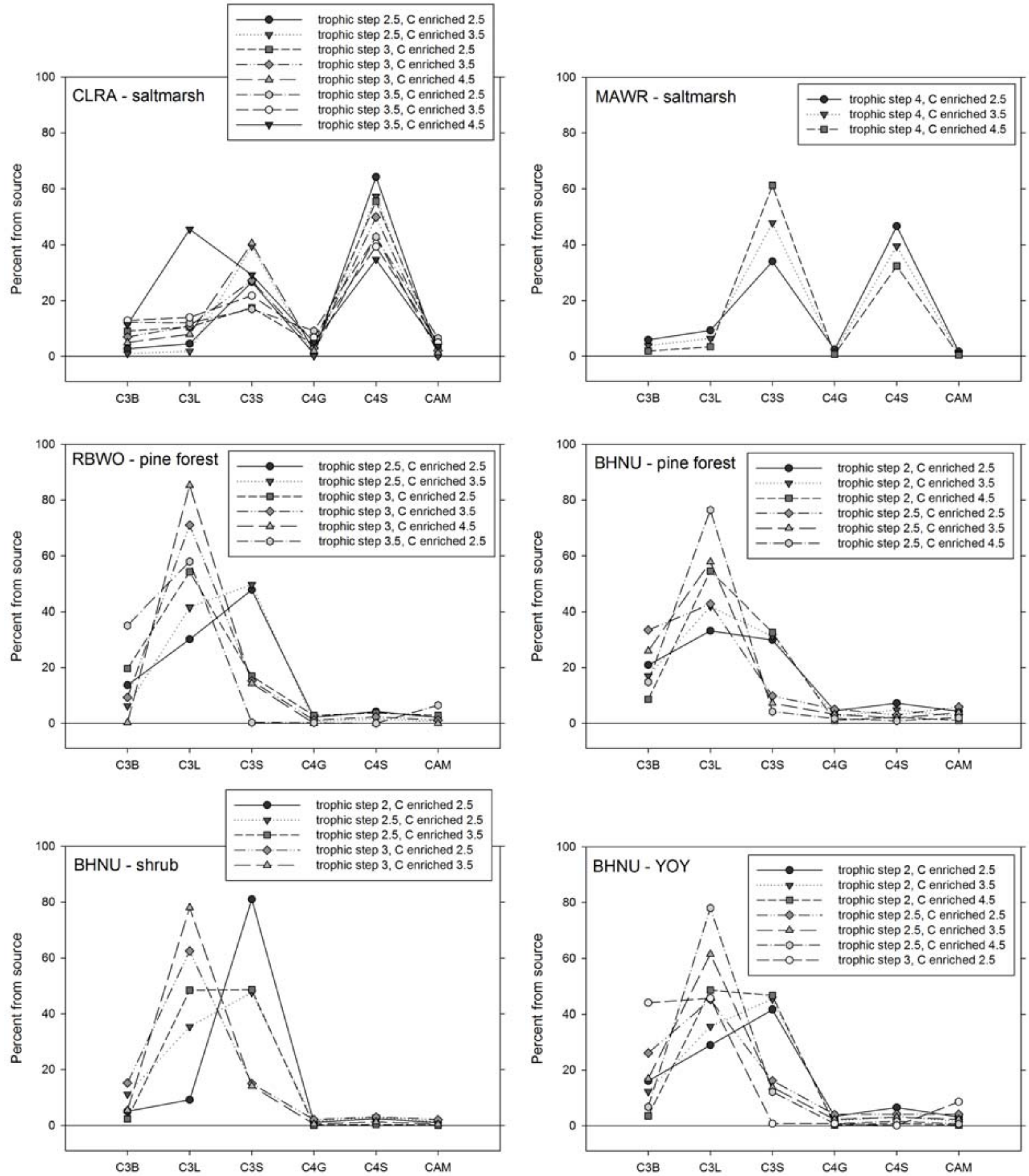
15
10
5
0
-5
-10
-32
-30
-28
-26
-24
-22
-20
-18
-16
-14
-12
Plants
Birds
Invertebrates
MAWR
CLRA
saCl
saH
PABU
EASO
CARW
RBWO
WEVI
YTWA
NOPA
BHNU pine
BHNU shrub
shC
opC
C4 Spartina
saD
C3 saltmarsh
shH
opH
shpD
oD
C3 leaves
C3 berries
C4 grasses
CAM plants
δ15N (‰)
δ13C (‰)

Figure 2.

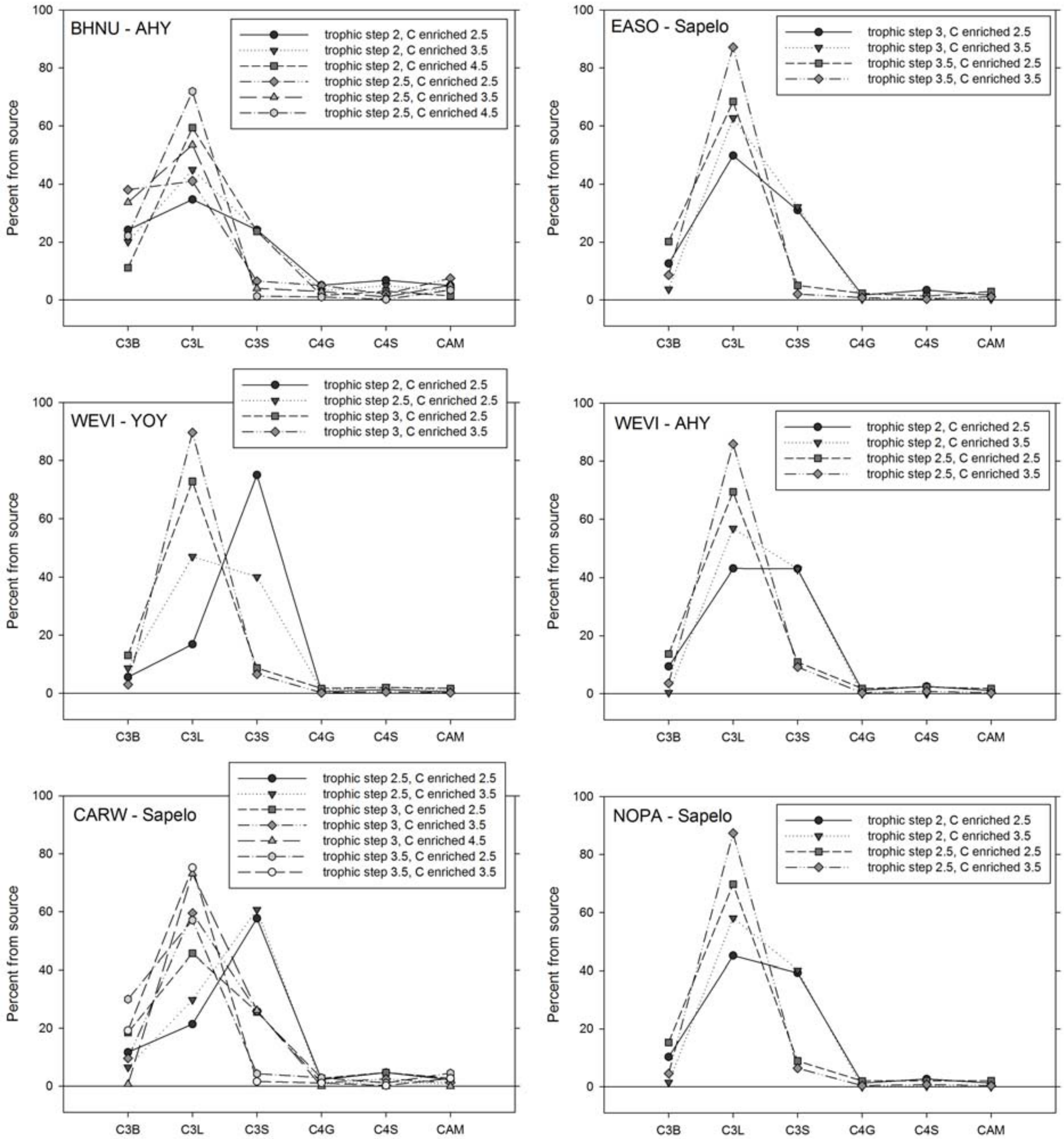


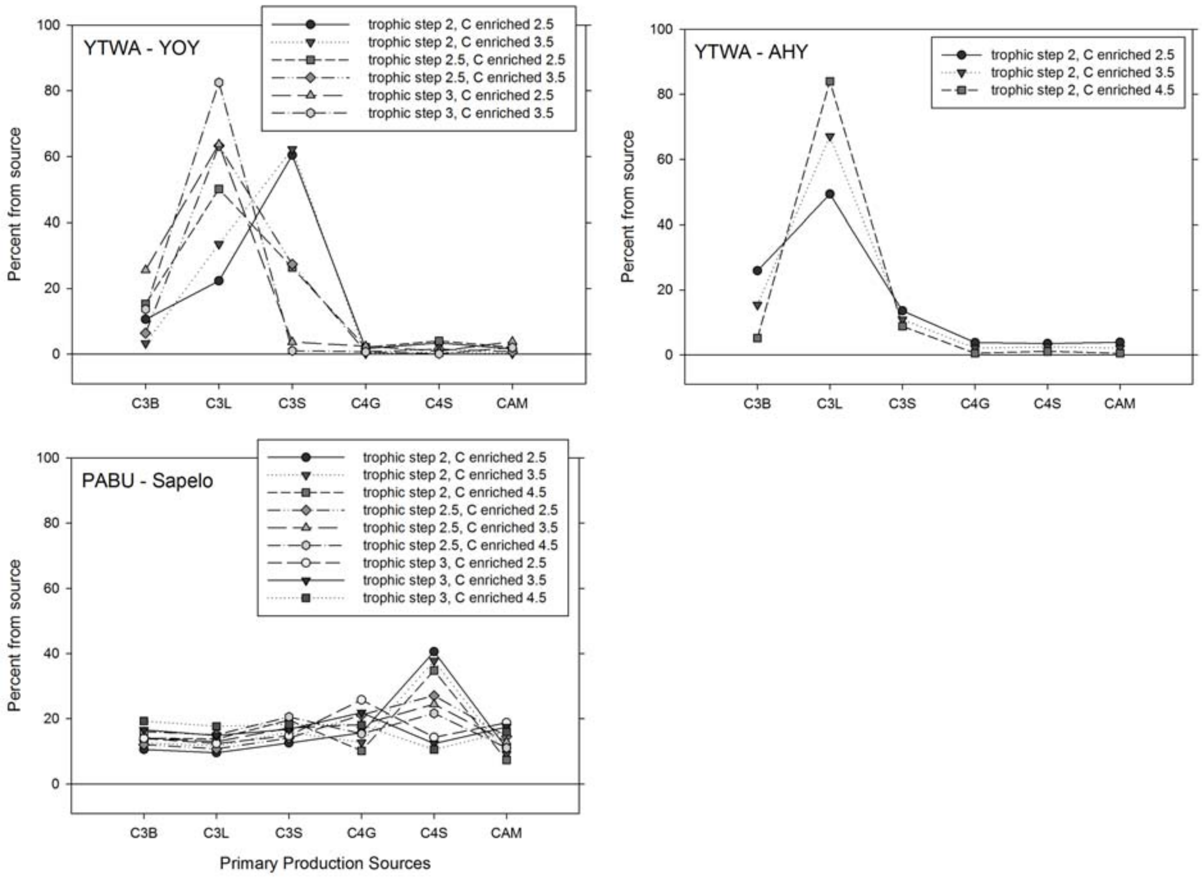
Birds
Plants
Invertebrates
CARW
NOPA
C
D
H
herbs
cypress
other
10
8
6
4
2
0
-36
-34
-32
-30
-28
-26
-24
-22
δ15N (‰)
δ13C (‰)

Figure 3.



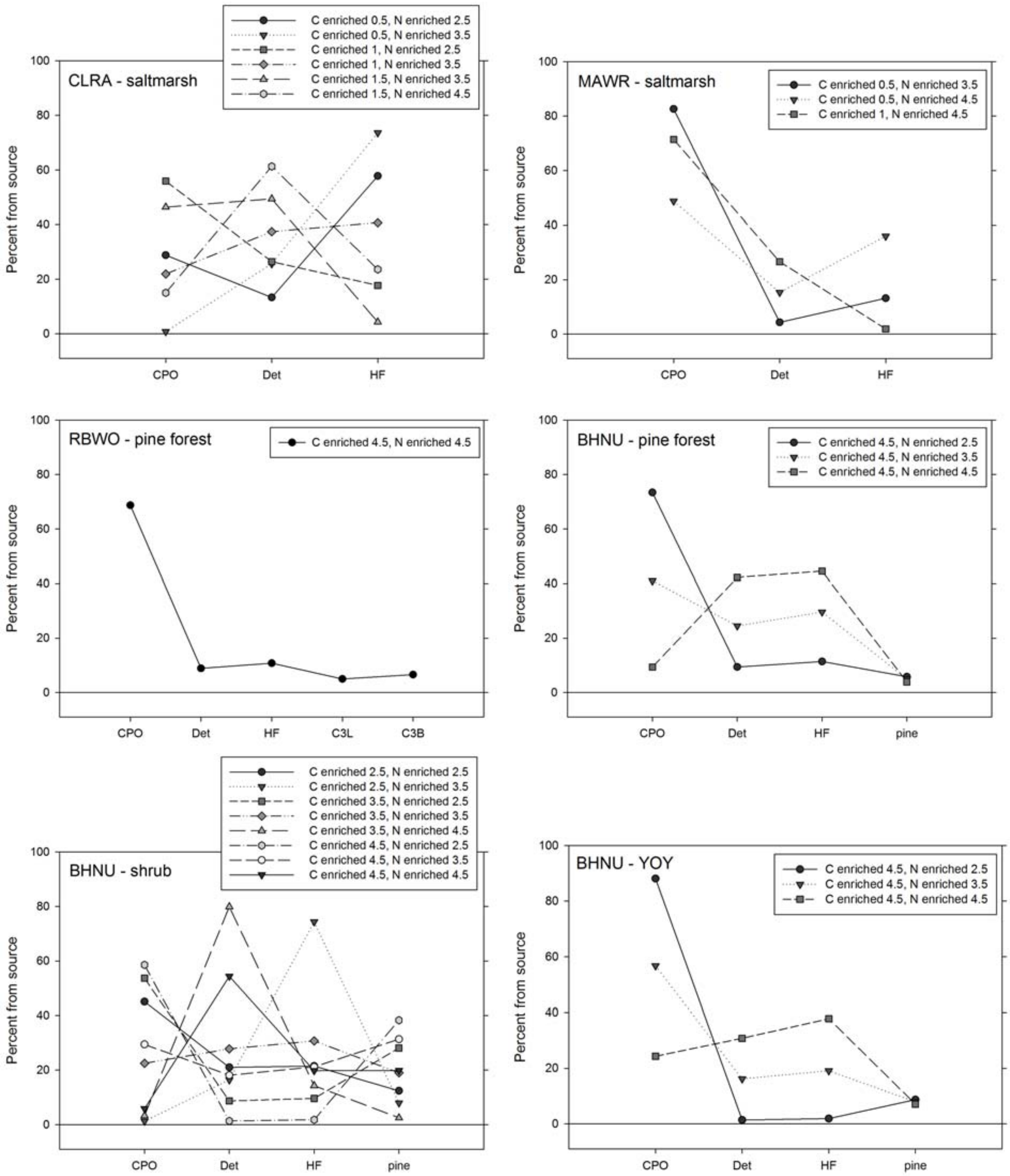
CLRA - saltmarsh
trophic step 2.5, C enriched 2.5
trophic step 2.5, C enriched 3.5
trophic step 3, C enriched 2.5
trophic step 3, C enriched 3.5
trophic step 3, C enriched 4.5
trophic step 3.5, C enriched 2.5
trophic step 3.5, C enriched 3.5
trophic step 3.5, C enriched 4.5
MAWR - saltmarsh
trophic step 4, C enriched 2.5
trophic step 4, C enriched 3.5
trophic step 4, C enriched 4.5
RBWO - pine forest
trophic step 2.5, C enriched 2.5
trophic step 2.5, C enriched 3.5
trophic step 3, C enriched 2.5
trophic step 3, C enriched 3.5
trophic step 3, C enriched 4.5
trophic step 3.5, C enriched 2.5
BHNU - pine forest
trophic step 2, C enriched 2.5
trophic step 2, C enriched 3.5
trophic step 2, C enriched 4.5
trophic step 2.5, C enriched 2.5
trophic step 2.5, C enriched 3.5
trophic step 2.5, C enriched 4.5
BHNU - shrub
trophic step 2, C enriched 2.5
trophic step 2.5, C enriched 2.5
trophic step 2.5, C enriched 3.5
trophic step 3, C enriched 2.5
trophic step 3, C enriched 3.5
BHNU - YOY
trophic step 2, C enriched 2.5
trophic step 2, C enriched 3.5
trophic step 2, C enriched 4.5
trophic step 2.5, C enriched 2.5
trophic step 2.5, C enriched 3.5
trophic step 2.5, C enriched 4.5
trophic step 3, C enriched 2.5
Percent from source
C3B
C3L
C3S
C4G
C4S
CAM

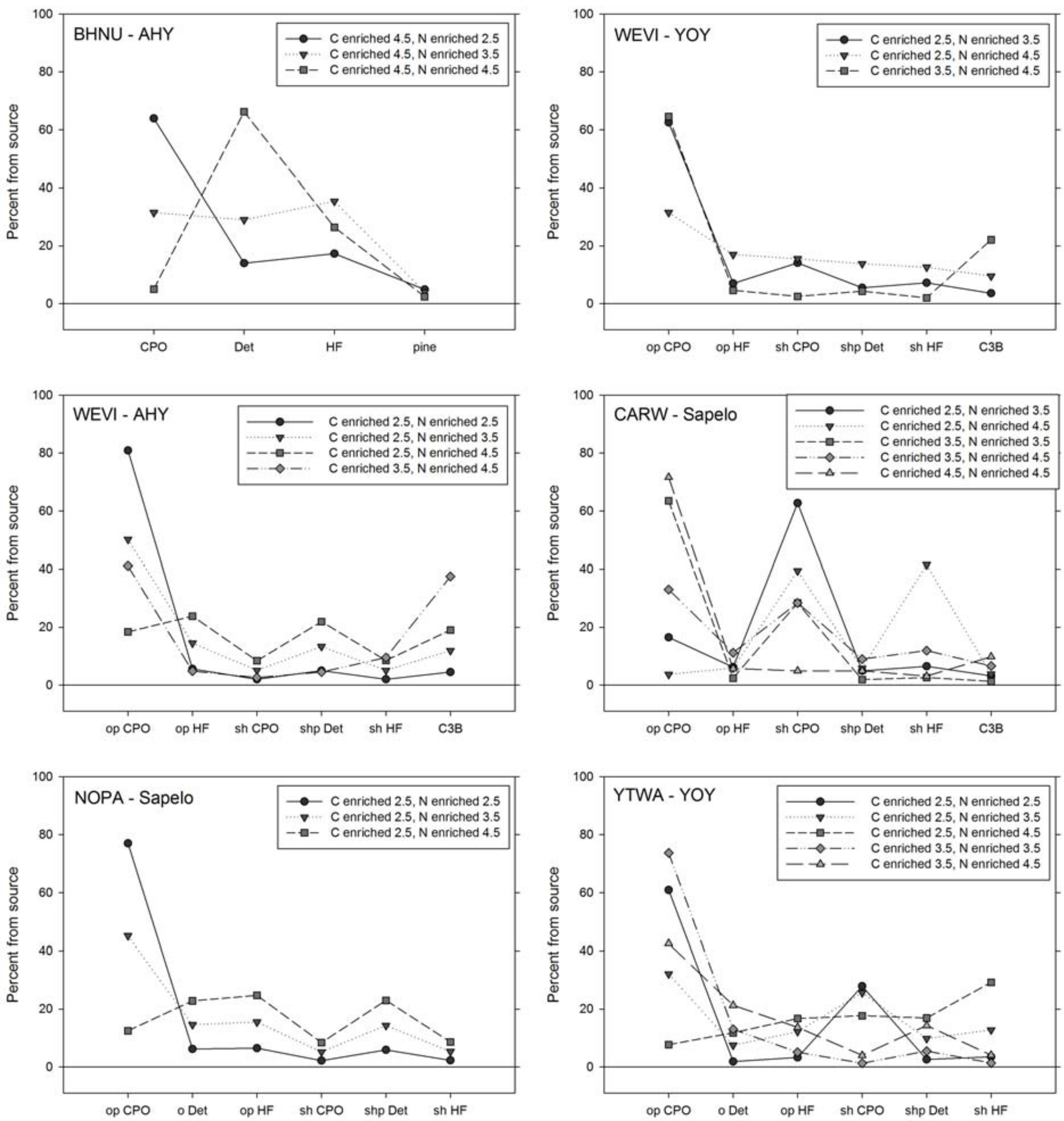

BHNU - AHY
trophic step 2, C enriched 2.5
trophic step 2, C enriched 3.5
trophic step 2, C enriched 4.5
trophic step 2.5, C enriched 2.5
trophic step 2.5, C enriched 3.5
trophic step 2.5, C enriched 4.5
EASO - Sapelo
trophic step 3, C enriched 2.5
trophic step 3, C enriched 3.5
trophic step 3.5, C enriched 2.5
trophic step 3.5, C enriched 3.5
WEVI - YOY
trophic step 2, C enriched 2.5
trophic step 2.5, C enriched 2.5
trophic step 3, C enriched 2.5
trophic step 3, C enriched 3.5
WEVI - AHY
trophic step 2, C enriched 2.5
trophic step 2, C enriched 3.5
trophic step 2.5, C enriched 2.5
trophic step 2.5, C enriched 3.5
CARW - Sapelo
trophic step 2.5, C enriched 2.5
trophic step 2.5, C enriched 3.5
trophic step 3, C enriched 2.5
trophic step 3, C enriched 3.5
trophic step 3, C enriched 4.5
trophic step 3.5, C enriched 2.5
trophic step 3.5, C enriched 3.5
NOPA - Sapelo
trophic step 2, C enriched 2.5
trophic step 2, C enriched 3.5
trophic step 2.5, C enriched 2.5
trophic step 2.5, C enriched 3.5
Percent from source
0
20
40
60
80
100
C3B
C3L
C3S
C4G
C4S
CAM

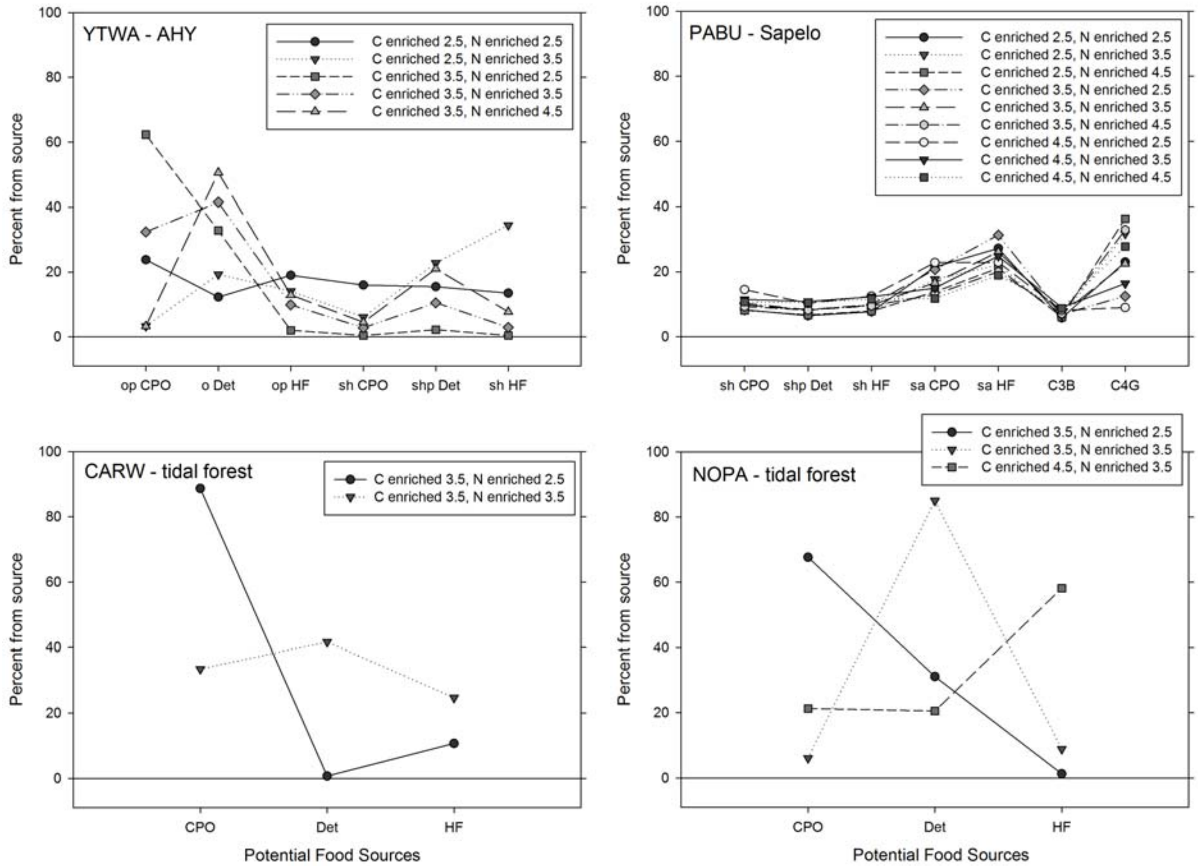


YTWA - YOY
trophic step 2, C enriched 2.5
trophic step 2, C enriched 3.5
trophic step 2.5, C enriched 2.5
trophic step 2.5, C enriched 3.5
trophic step 3, C enriched 2.5
trophic step 3, C enriched 3.5
Percent from source
0
20
40
60
80
100
C3B
C3L
C3S
C4G
C4S
CAM
YTWA - AHY
trophic step 2, C enriched 2.5
trophic step 2, C enriched 3.5
trophic step 2, C enriched 4.5
PABU - Sapelo
trophic step 2, C enriched 2.5
trophic step 2, C enriched 3.5
trophic step 2, C enriched 4.5
trophic step 2.5, C enriched 2.5
trophic step 2.5, C enriched 3.5
trophic step 2.5, C enriched 4.5
trophic step 3, C enriched 2.5
trophic step 3, C enriched 3.5
trophic step 3, C enriched 4.5
Primary Production Sources

Figure 4.


CLRA - saltmarsh
C enriched 0.5, N enriched 2.5
C enriched 0.5, N enriched 3.5
C enriched 1, N enriched 2.5
C enriched 1, N enriched 3.5
C enriched 1.5, N enriched 3.5
C enriched 1.5, N enriched 4.5
Percent from source
CPO
Det
HF
MAWR - saltmarsh
C enriched 0.5, N enriched 3.5
C enriched 0.5, N enriched 4.5
C enriched 1, N enriched 4.5
Percent from source
CPO
Det
HF
RBWO - pine forest
C enriched 4.5, N enriched 4.5
Percent from source
CPO
Det
HF
C3L
C3B
BHNU - pine forest
C enriched 4.5, N enriched 2.5
C enriched 4.5, N enriched 3.5
C enriched 4.5, N enriched 4.5
Percent from source
CPO
Det
HF
pine
BHNU - shrub
C enriched 2.5, N enriched 2.5
C enriched 2.5, N enriched 3.5
C enriched 3.5, N enriched 2.5
C enriched 3.5, N enriched 3.5
C enriched 3.5, N enriched 4.5
C enriched 4.5, N enriched 2.5
C enriched 4.5, N enriched 3.5
C enriched 4.5, N enriched 4.5
Percent from source
CPO
Det
HF
pine
BHNU - YOY
C enriched 4.5, N enriched 2.5
C enriched 4.5, N enriched 3.5
C enriched 4.5, N enriched 4.5
Percent from source
CPO
Det
HF
pine


BHNU - AHY
C enriched 4.5, N enriched 2.5
C enriched 4.5, N enriched 3.5
C enriched 4.5, N enriched 4.5
Percent from source
CPO
Det
HF
pine
WEVI - YOY
C enriched 2.5, N enriched 3.5
C enriched 2.5, N enriched 4.5
C enriched 3.5, N enriched 4.5
op CPO
op HF
sh CPO
shp Det
sh HF
C3B
WEVI - AHY
C enriched 2.5, N enriched 2.5
C enriched 2.5, N enriched 3.5
C enriched 2.5, N enriched 4.5
C enriched 3.5, N enriched 4.5
CARW - Sapelo
C enriched 2.5, N enriched 3.5
C enriched 2.5, N enriched 4.5
C enriched 3.5, N enriched 3.5
C enriched 3.5, N enriched 4.5
C enriched 4.5, N enriched 4.5
NOPA - Sapelo
C enriched 2.5, N enriched 2.5
C enriched 2.5, N enriched 3.5
C enriched 2.5, N enriched 4.5
op CPO
o Det
op HF
sh CPO
shp Det
sh HF
YTWA - YOY
C enriched 2.5, N enriched 2.5
C enriched 2.5, N enriched 3.5
C enriched 2.5, N enriched 4.5
C enriched 3.5, N enriched 3.5
C enriched 3.5, N enriched 4.5



YTWA - AHY
C enriched 2.5, N enriched 2.5
C enriched 2.5, N enriched 3.5
C enriched 3.5, N enriched 2.5
C enriched 3.5, N enriched 3.5
C enriched 3.5, N enriched 4.5
Percent from source
op CPO
o Det
op HF
sh CPO
shp Det
sh HF
PABU - Sapelo
C enriched 2.5, N enriched 2.5
C enriched 2.5, N enriched 3.5
C enriched 2.5, N enriched 4.5
C enriched 3.5, N enriched 2.5
C enriched 3.5, N enriched 3.5
C enriched 3.5, N enriched 4.5
C enriched 4.5, N enriched 2.5
C enriched 4.5, N enriched 3.5
C enriched 4.5, N enriched 4.5
sh CPO
shp Det
sh HF
sa CPO
sa HF
C3B
C4G
CARW - tidal forest
C enriched 3.5, N enriched 2.5
C enriched 3.5, N enriched 3.5
CPO
Det
HF
Potential Food Sources
NOPA - tidal forest
C enriched 3.5, N enriched 2.5
C enriched 3.5, N enriched 3.5
C enriched 4.5, N enriched 3.5

Figure 5.

Appendix 1. Sample size (N), mean $\delta^{13}C$ (in ‰) and $\delta^{15}N$ (in ‰) ± 1 SE of plants sampled in five habitats of coastal Georgia in 2006 and 2007. See text for scientific names of plants. Standard errors have been additively propagated with the instrument error (0.059‰ for $\delta^{13}C$ and 0.157‰ for $\delta^{15}N$).

	Tidal forest			Saltmarsh			Shrub			Oak forest			Pine forest		
	N	$\delta^{13}C$	$\delta^{15}N$	N	$\delta^{13}C$	$\delta^{15}N$	N	$\delta^{13}C$	$\delta^{15}N$	N	$d^{13}C$	$\delta^{15}N$	N	$\delta^{13}C$	$\delta^{15}N$
andropogon							3	-13.54 ±0.26	-2.4 ±0.6						
redbay							1	-30.44 ±0.06	-1.0 ±0.2	4	-30.73 ±0.68	-2.8 ±0.9			
borrichia				4	-27.00 ±0.71	0.9 ±1.2									
borrichia flowers				2	-27.07 ±0.81	1.2 ±1.0									
red cedar							6	-27.33 ±0.67	-3.1 ±0.3						
red cedar berries							6	-25.13 ±0.36	-1.8 ±0.7						
bald cypress	6	-30.56 ±0.69	3.0 ±0.7												
dog fennel							3	-28.02 ±0.18	-1.6 ±0.4						
sweet gum	6	-32.47 ±0.30	0.7 ±0.5												
american holly	1	-31.32 ±0.06	-3.5 ±0.2							5	-30.63 ±0.30	-1.8 ±1.0			
am. holly berries										5	-29.94 ±0.74	-2.8 ±0.5			
black needlerush	3	-24.56 ±0.14	3.4 ±1.0												
needlerush flowers	2	-28.68 ±1.02	-0.9 ±0.9												
live oak										6	-31.30 ±0.21	-0.7 ±0.7			

lizard tail	3	-34.27 ±0.24	2.7 ±0.2												
lizard tail seeds	3	-33.97 ±0.50	3.3 ±0.7												
loblolly pine													6	-30.20 ±0.59	-2.2 ±0.7
muhly grass							2	-13.35 ±0.11	-2.4 ±0.6						
wax myrtle							6	-29.05 ±0.81	-1.3 ±0.4	3	-30.00 ±0.54	-0.5 ±0.1	6	-30.48 ±0.56	-1.4 ±0.5
wax myrtle berries							4	-27.09 ±0.86	-2.6 ±0.7						
water oak	6	-31.49 ±0.13	0.8 ±0.6												
blue palm	6	-31.35 ±0.22	1.3 ±1.0												
saw palmetto													6	-30.51 ±0.59	1.3 ±0.6
panicum	3	-32.53 ±0.64	1.8 ±0.7												
salicornia				4	-27.35 ±0.92	4.4 ±0.9									
slash pine													2	-28.90 ±0.43	-3.0 ±1.6
spanish moss										6	-16.08 ±0.35	-5.9 ±0.3			
smooth cordgrass				8	-13.92 ±0.33	5.6 ±0.5									
tupelo gum	3	-32.75 ±0.82	1.7 ±0.9												
yaupon							5	-27.94 ±0.94	-2.9 ±0.6				6	-30.08 ±0.50	-0.8 ±0.7
yaupon berries							5	-27.14 ±0.95	-2.8 ±0.5				4	-28.92 ±0.53	-1.0 ±0.6

Appendix 2. Sample size (N), mean $\delta^{13}C$ (in ‰) and mean $\delta^{15}N$ (in ‰) ± 1 SE of invertebrates sampled in five habitats of coastal Georgia in 2006 and 2007. Only invertebrates that were present in at least 50% of the sites in a habitat were isotopically analysed. Sample sizes represent the number of drops in the mass spectrometer, but the number of invertebrates in any given drop varied. Standard errors have been additively propagated with the instrument error (0.059‰ for $\delta^{13}C$ and 0.157‰ for $\delta^{15}N$).

	Tidal forest					Saltmarsh					Shrub					Oak forest					Pine forest				
	N	$\delta^{13}C$	SE	$\delta^{15}N$	SE	N	$\delta^{13}C$	SE	$\delta^{15}N$	SE	N	$\delta^{13}C$	SE	$\delta^{15}N$	SE	N	$\delta^{13}C$	SE	$\delta^{15}N$	SE	N	$\delta^{13}C$	SE	$\delta^{15}N$	SE
acarina																					3	-27.14	0.10	-2.0	0.8
araneae nephila clavipes	6	-26.86	0.45	4.7	0.4																				
araneae phalangiidae	8	-29.09	0.32	5.2	0.1						2	-26.87	0.21	3.9	1.3						3	-26.37	0.73	1.9	0.6
araneae salticidae	3	-28.36	0.49	4.2	0.8						6	-22.63	1.09	4.7	1.1						2	-25.83	1.78	5.4	1.0
araneae ssp.	9	-29.67	0.43	5.4	0.4	14	-16.54	1.70	6.1	1.9	8	-23.51	0.79	3.2	0.6	9	-26.31	0.22	1.4	0.3	10	-25.97	0.25	3.0	0.5
blattaria egg																3	-27.73	0.30	-1.3	0.1					
coleoptera alleculidae																3	-25.70	0.33	1.4	0.4					
coleoptera buprestidae											3	-26.25	1.69	5.2	0.4										
coleoptera chrysomelidae	9	-30.94	1.05	2.8	0.8						11	-22.48	1.14	2.4	0.5						1	-26.72	0.06	3.5	0.2
coleoptera ciidae																2	-25.61	1.01	-0.3	0.4					
coleoptera cleridae						3	-14.08	0.24	9.6	0.4															
coleoptera coccinellidae																					3	-30.29	0.47	5.1	1.1
coleoptera curculionidae	2	-29.51	2.29	4.3	1.7						5	-25.66	2.03	1.5	0.2	4	-27.43	0.18	2.3	0.6					

coleoptera elateridae																3	-25.25	1.39	4.8	0.9					
coleoptera mordellidae	2	-26.12	0.30	1.4	0.3	3	-11.87	0.23	7.4	0.7	6	-24.09	1.02	2.2	0.4	4	-24.96	0.51	1.3	0.6					
coleoptera phalacridae											4	-24.54	0.44	1.8	0.2										
diplopoda	3	-26.28	0.33	1.3	0.5																				
diptera bibionidae											3	-24.65	0.18	5.1	0.4										
diptera culicidae	3	-28.59	0.24	5.1	0.7																				
diptera dolichopodidae	7	-27.68	0.47	6.0	0.4						2	-22.20	1.63	7.4	0.7	4	-24.95	0.35	7.0	0.5	6	-25.14	0.34	5.9	0.4
diptera tephritidae						6	-14.45	0.35	9.3	0.6															
diptera tipulidae	5	-27.06	0.42	4.3	0.7																				
heteroptera alydidae											3	-28.35	1.37	4.2	0.9										
heteroptera lygaeidae	2	-30.57	0.53	3.2	1.3											2	-28.24	0.08	1.8	0.9					
heteroptera miridae						3	-13.61	0.09	9.7	0.6											3	-26.58	0.51	2.2	0.9
heteroptera pentatomidae											2	-22.83	5.35	0.9	0.6										
heteroptera reduviidae											3	-24.91	1.16	5.1	0.7										
homoptera aphididae																					3	-28.35	1.37	0.1	0.2
homoptera cercopidae						2	-13.92	0.05	10.7	0.4	5	-24.16	1.18	1.5	1.0										
homoptera cicadellidae	8	-29.16	0.70	2.8	0.7						9	-25.47	0.48	1.1	0.5	3	-29.24	0.13	1.5	0.5	2	-28.39	0.45	0.6	0.7
homoptera cixiidae	6	-27.54	0.30	2.2	1.4																				
homoptera delphacidae	3	-32.42	0.52	4.0	0.1	6	-14.17	0.20	6.8	0.3															

homoptera flatidae											3	-24.39	0.79	0.5	0.4										
homoptera ortheziidae																1	-15.83	0.06	-3.7	0.2					
hymenoptera braconidae	5	-26.84	0.48	6.0	0.6						4	-25.28	1.26	4.2	1.2	7	-26.71	0.28	3.4	0.6	2	-25.54	0.09	3.3	0.2
hymenoptera eurytomidae						2	-12.89	0.24	13.0	1.9	2	-19.07	0.24	5.4	0.4										
hymenoptera formicidae	4	-28.06	0.31	4.6	0.4	5	-13.67	0.22	11.0	0.6	6	-23.75	0.81	3.5	0.4	2	-27.56	0.46	2.6	1.0	3	-24.86	0.65	3.4	0.8
hymenoptera sphecidae											3	-21.33	1.77	9.1	3.0										
hymenoptera tiphiidae											3	-23.12	1.01	8.1	0.5										
hypsogastropoda littorinidae						6	-13.67	0.12	6.9	0.3															
lepidoptera larvae											1	-27.94	0.06	3.5	0.2	1	-13.20	0.06	0.5	0.2	1	-28.78	0.06	0.1	0.2
lepidoptera moth	2	-28.86	0.53	4.6	1.2						5	-27.34	1.10	2.0	0.5	3	-29.00	1.32	0.4	0.9	2	-28.01	0.90	4.5	0.6
lepidoptera nymphalidae											3	-28.67	0.28	0.5	1.4										
mantodea mantidae	2	-27.60	1.99	4.8	0.5						5	-23.82	0.71	3.9	0.4										
ocypodidae uca pugnax						6	-16.32	0.49	4.4	0.4															
orthoptera acrididae											2	-27.70	1.69	3.1	1.5										
orthoptera gryllidae	12	-28.63	0.39	3.8	0.6						4	-26.04	0.43	-1.1	1.2	4	-26.00	0.54	-2.9	0.6	2	-26.96	0.84	-1.2	0.2
orthoptera tetrigidae	2	-27.49	0.47	1.4	0.1																				
orthoptera tettigoniidae	7	-28.83	0.88	4.1	0.8						4	-21.77	2.44	0.8	0.4	1	-14.45	0.06	-0.4	0.2					
orchelimum fidicinium						6	-15.23	0.58	8.4	0.6															
psocoptera psocidae											4	-26.46	0.29	-2.0	0.6	6	-27.69	0.24	-1.5	0.3	10	-27.13	0.13	-0.7	0.4

thysanoptera	1	-13.29	0.06	6.3	0.2

Appendix 3. Sample size (N), mean $\delta^{13}C$ (in ‰) and $\delta^{15}N$ (in ‰) ± 1 SE of bird feathers sampled in coastal Georgia in 2006 and 2007 by capture and age of feather. Bird captures are categorized by the original capture of the birds compared to birds that were recaptured at a later date with feathers grown from a different time period. Feather age is categorized by feathers grown in an unknown location versus those that were fresh at the time of capture and assumed to have grown in the capture location. See text for scientific names of bird species. Standard errors have been additively propagated with the instrument error (0.059‰ for $\delta^{13}C$ and 0.157‰ for $\delta^{15}N$).

	Bird Captures						Feather Age					
	Original capture			Recapture			Fresh feathers			Old feathers		
	N	$\delta^{13}C$	$\delta^{15}N$	N	$\delta^{13}C$	$\delta^{15}N$	N	$\delta^{13}C$	$\delta^{15}N$	N	$\delta^{13}C$	$\delta^{15}N$
Clapper Rail							2	-12.93 ±0.14	11.7 ±0.1	2	-15.15 ±1.08	9.6 ±0.1
Eastern Screech Owl							7	-22.45 ±0.33	7.3 ±0.4	21	-22.45 ±0.18	7.4 ±0.2
Red-bellied Woodpecker							3	-22.67 ±0.47	6.5 ±0.6	10	-22.31 ±0.16	6.8 ±0.2
Brown-headed Nuthatch	54	22.23 ±0.09	5.2 ±0.1	2	-21.49 ±0.20	4.7 ±0.9	26*	-22.21 ±0.10	5.6 ±0.2	30	-22.20 ±0.15	4.7 ±0.1
Carolina Wren							4	-22.73 ±0.15	6.0 ±0.4	30	-22.87 ±0.32	7.6 ±0.2
Marsh Wren							1	-22.16 ±0.06	9.1 ±0.2	17	-13.76 ±0.81	13.1 ±0.3
Northern Parula	75	-23.78 ±0.07	6.0 ±0.2	15	-23.90 ±0.17	5.3 ±0.6	7	-23.72 ±0.17	5.6 ±1.3	83	-23.81 ±0.07	5.9 ±0.2
White-eyed Vireo							25*	-23.34 ±0.17	6.6 ±0.1	21	-23.75 ±0.25	5.4 ±0.1
Yellow-throated Warbler							14*	-22.91 ±0.09	6.1 ±0.2	16	-23.60 ±0.14	4.3 ±0.2
Painted Bunting							5	-16.47 ±2.18	7.4 ±1.5	35	-14.65 ±0.69	6.5 ±0.4

* indicates isotopic results that are different between habitats for each species based on Multi Response Permutation Procedures, corrected using sequential Bonferroni methods ($\alpha = 0.05$).

Appendix 4. Sample size (N), mean $\delta^{13}C$ (in ‰) and $\delta^{15}N$ (in ‰) ± 1 SE of bird feathers sampled in coastal Georgia in 2006 and 2007 by sex of the bird. Sex was determined by the presence/absence of a cloacal protuberance or brood patch for species with no obvious sexual dimorphism. See text for scientific names of bird species. Standard errors have been additively propagated with the instrument error (0.059‰ for $\delta^{13}C$ and 0.157‰ for $\delta^{15}N$).

	Female			Male			Unknown		
	N	$\delta^{13}C$	$\delta^{15}N$	N	$\delta^{13}C$	$\delta^{15}N$	N	$\delta^{13}C$	$\delta^{15}N$
Clapper Rail							4	-14.04 ±0.78	10.6 ±0.6
Eastern Screech Owl				1	-25.35 ±0.06	8.3 ±0.2	27	-22.35 ±0.12	7.4 ±0.2
Red-bellied Woodpecker	2	-23.48 ±0.12	5.4 ±0.2	11	-22.20 ±0.10	7.0 ±0.2			
Brown-headed Nuthatch	15[a]	-22.29 ±0.20	4.8 ±0.2	7[a]	-22.56 ±0.24	4.8 ±0.4	34[b]	-22.09 ±0.11	5.3 ±0.1
Carolina Wren	8[a]	-21.91 ±0.57	6.9 ±0.4	18[b]	-23.24 ±0.44	7.6 ±0.2	7[a,b]	-23.03 ±0.30	7.3 ±0.5
Marsh Wren	6	-14.09 ±1.93	12.4 ±0.9	12	-14.30 ±1.00	13.1 ±0.2			
Northern Parula	10[a]	-23.84 ±0.26	5.1 ±0.3	80[b]	-23.80 ±0.06	5.9 ±0.2			
White-eyed Vireo	10[a]	-23.72 ±0.35	5.5 ±0.2	11[a]	-23.77 ±0.36	5.2 ±0.2	25[b]	-23.34 ±0.17	6.6 ±0.1
Yellow-throated Warbler	2[a,b]	-23.77 ±0.57	4.9 ±0.2	14[a]	-23.57 ±0.14	4.4 ±0.3	14[b]	-22.91 ±0.09	6.1 ±0.2
Painted Bunting	9	-17.11 ±1.46	6.5 ±0.9	28	-13.98 ±0.74	6.6 ±0.5	3	-16.47 ±2.25	7.9 ±2.2

[a and b] indicate isotopic results that are alike among sex categories for each species based on Multi Response Permutation Procedures, corrected using sequential Bonferroni methods at alpha = 0.05.

ELUCIDATING AVIAN FOOD WEBS OF TERRESTRIAL AND WETLAND HABITATS OF COASTAL GEORGIA, USA, USING STABLE ISOTOPES OF ^{13}C AND ^{15}N

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Abstract. Avian conservation requires linking populations to their respective food sources, but few studies have investigated passerine food webs using stable isotopes. $\delta^{13}C$ and $\delta^{15}N$ were used to identify potential sources of primary production at the base of the food web and direct consumption of prey for avifauna of five habitats in coastal Georgia, tidal-freshwater forest, saltmarsh, maritime scrub-shrub, maritime broadleaf and maritime narrowleaf forests. Primary production sources on Sapelo Island, Georgia included C_3 berries ($\delta^{13}C$ = -27.51 and $\delta^{15}N$ = -2.2), C_3 leaves ($\delta^{13}C$ = -29.74 and $\delta^{15}N$ = -1.5), CAM plants ($\delta^{13}C$ = -16.08 and $\delta^{15}N$ = -5.9), C_4 terrestrial grasses ($\delta^{13}C$ = -13.46 and $\delta^{15}N$ = -2.4), C_3 saltmarsh vegetation ($\delta^{13}C$ = -26.84 and $\delta^{15}N$ = 1.8) and C_4 saltmarsh vegetation ($\delta^{13}C$ = -13.92 and $\delta^{15}N$ = 5.6). Saltmarsh species, such as Clapper Rail and Marsh Wren, exhibited high fidelity to saltmarsh food sources ($\delta^{13}C$ = -14.04 and $\delta^{15}N$ = 10.6, and $\delta^{13}C$ = -14.23 and $\delta^{15}N$ = 12.9). Birds from shrub habitat and Marsh Wrens from saltmarsh derived a large portion of their food web from the C_3 saltmarsh vegetation at the terrestrial ecotone outside of their associated habitats, indicating dynamic trophic overlap of the C_3 saltmarsh vegetation with adjacent C_4 saltmarsh and shrub habitats. Most terrestrial species of birds, such as Northern Parula and Brown-headed Nuthatch, appeared to derive most of their food webs from the terrestrial habitats they occupy ($\delta^{13}C$ = -23.75 and $\delta^{15}N$ = 5.4, and $\delta^{13}C$ = -22.20 and $\delta^{15}N$ = 5.2). Painted Buntings, the species of highest conservation concern in the region, were isotopically more similar to the saltmarsh species than other terrestrial species ($\delta^{13}C$ = -14.87 and $\delta^{15}N$ = 6.7). Marsh Wrens are likely feeding on spiders that prey upon flying insects (e.g., diptera) that originated in the C3 saltmarsh vegetation at the terrestrial ecotone, while Painted Buntings appear to forage within the marsh. Avian conservation efforts in coastal Georgia may need to include nearby saltmarsh habitat for terrestrial-associated species during the breeding season.

Key words: carbon isotopes, nitrogen isotopes, prey, Isosource, Georgia, guild, passerines, rail, screech owl, trophic position, food web, habitat

INTRODUCTION

Avian conservation requires linking populations to their respective food webs (Hobson and Wassenaar 1997). Conventional avian mark-recapture techniques rarely provide statistically valid information on trophic dynamics (Hobson et al. 2004a), but conventional techniques supplemented with stable isotope data may aid in the interpretation of trophic relationships and habitat use of these species (Hobson et al. 1994, Kelly 2000). Many studies have investigated seabird trophic webs using stable isotopes (Duxbury and Holroyd 1997, Cherel et al. 2000, Kelly 2000, Harding and Stevens 2001, Hobson et al. 2004), but relatively few studies have investigated passerine food webs (Kelly 2000).

Effective avian conservation requires identifying seasonal primary feeding locations and food sources (Hobson et al. 2004b, Pain et al. 2004, Rubenstein and Hobson 2004). Conventional dietary analysis techniques (e.g., stomach content) can be harmful or fatal to individuals and may be biased by organisms that are not readily digested (Kelly 2000). Stable isotopes have the ability to assess species-habitat relationships with minimal risk to rare or threatened species.

Stable isotopic composition of avifauna tissues, including feathers, reflects the average value of each stable isotope ratio found in source materials used to grow the tissues, such as food ingested during the period of tissue growth and stored biomass (Duxbury and Holroyd 1997). The ratio of $^{13}C/^{12}C$ in feathers (expressed as $\delta^{13}C$ values in ‰ units) can be used to infer avian food sources due to differences in $\delta^{13}C$ between C_3, CAM and C_4 photosynthetic pathways (Bearhop et al. 2004). Food from primary production reaches birds through either direct herbivory or through transformed animal biomass in carnivory, with varying ^{13}C-enrichment rates at each trophic level that must be accounted for (Kelly 2000, Pearson et al. 2003). Animals typically increase $\delta^{13}C$ in whole body tissues by ~0.5‰ for each trophic level in their diet (Post 2002), ranging from no enrichment to as much as 1.6‰ in invertebrates (Langellotto et al. 2005).

A recent study of Yellow-rumped Warblers (*Dendroica coronata*) showed feathers ^{13}C-enriched by 1.9‰ when insects were a small part of their diet and up to 4.3‰ with near-complete insectivory (Pearson et al. 2003). Nitrogen stable isotope ratios ($\delta^{15}N$) show a similar systematic 3-5‰ ^{15}N-enrichment with each increase in trophic level. The ^{15}N-enrichment is less variable among body tissues than ^{13}C and reveals information about an organism's trophic position (e.g., primary or secondary consumer; Peterson et al. 1985, Ambrose 1993, Harding and Stevens 2001).

In order for stable isotope analysis to trace trophic webs, tissue samples (e.g., feathers) must have grown from source materials originating from the location of interest, and potential food sources within the trophic web must exhibit differences in their stable isotopic signature during the time period the food was ingested or sources will not be able to be partitioned (Peterson and Fry 1987, Bearhop et al. 2004). Organisms feeding on a wide range of prey items from multiple trophic levels and/or geographic regions exhibit correspondingly higher variation in isotopic composition, as will populations with varying individual diets (Bearhop et al. 2004). Multiple stable-isotope analyses can also determine the degree of fidelity species have to certain habitats (Peterson and Fry 1987).

We used stable isotope analysis techniques to characterize foraging habitats and trophic dynamics for at least two target bird species in each of five habitats in coastal Georgia, USA [Northern Parula (*Parula Americana* (Linnaeus, 1758)) and Carolina Wren (*Thryothorus ludovicianus* (Latham, 1790)) in tidal-freshwater forest; Clapper Rail (*Rallus longirostris* (Boddeart, 1783)) and Marsh Wren (*Cistothorus palustris* (A. Wilson, 1810)) in saltmarsh; White-eyed Vireo (*Vireo griseus* (Boddeart, 1783)) and Painted Bunting (*Passerina ciris* (Linnaeus, 1758)) in maritime scrub-shrub; Northern Parula, Yellow-throated Warbler (*Dendroica dominica* (Linnaeus, 1766)) and Eastern Screech Owl (*Megascops asio* (Linnaeus, 1758)) in maritime broadleaf forest; and Red-bellied Woodpecker (*Melanerpes carolinus* (Linnaeus, 1758)), Brown-headed Nuthatch (*Sitta pusilla* Latham, 1790) and Eastern Screech Owl in maritime narrowleaf forest]. The goal of this study is to elucidate food sources for the ten species to recommend avian-habitat conservation strategies and to evaluate potential effects of management practices on avian food resource availability.

METHODS

Study Area

Five habitats, tidal-freshwater broadleaf deciduous forest, saltmarsh, maritime scrub-shrub, maritime broadleaf evergreen forest, and maritime narrowleaf evergreen forest, were sampled in coastal Georgia, USA (Figure 1). Tidal-freshwater forest (tidal forest) is located in the Clayhole Swamp Wildlife Management Area in Glynn County, Georgia, owned and managed by the Georgia Department of Natural Resources, and is dominated by C_3 photosynthetic plants, bald cypress (*Taxodium distichum* (L.) Rich.) and tupelo gum (*Nyssa aquatic* L.). Saltmarsh, maritime scrub-shrub (shrub), maritime broadleaf evergreen forest (oak forest) and maritime narrowleaf evergreen forest (pine forest) are all located on 6,677 ha Sapelo Island, McIntosh County, Georgia, on property jointly owned and managed by the Georgia Department of Natural Resources and the Sapelo Island National Estuarine Research Reserve. Dominant species included smooth cordgrass (*Spartina alterniflora* Loisel., a C_4 plant), in saltmarsh, wax myrtle (*Morella cerifera* (L.) Small) in shrub habitat, live oak (*Quercus virginiana* P. Mill.) in oak forest, and loblolly pine (*Pinus taeda* L.) in pine forest. In shrub habitat the herbaceous layer was also dominated by various C_4 grasses and oak forest was covered with epiphytic Spanish moss (*Tillandsia usnoides* (L.) L., a CAM plant). See Brittain et al. (2009b) for details on the site locations.

Vegetation, Invertebrate and Bird Sampling

Vegetation was sampled by collecting the whole stems of herbaceous plants or clippings off small branches of woody vegetation at ten sites per habitat. Invertebrates were sampled by sweeping the outer foliage of multiple plants of the same species (up to 12 feet) for three minutes with a net. Fiddler crabs (*Uca pugnax* (S. I. Smith, 1870)) were sampled by hand at each of the saltmarsh sites. Capture and banding were attempted for at least two target species of birds at each of the sample sites in each habitat type. Target species include: Northern Parula and Carolina Wren in tidal forest; Marsh Wren and Clapper Rail in saltmarsh; Eastern Screech Owl, Painted Bunting and White-eyed Vireo in shrub; Eastern Screech Owl, Northern Parula and Yellow-throated Warbler in oak forest; and, Eastern Screech Owl, Brown-headed Nuthatch and Red-bellied Woodpecker in pine forest. See Brittain et al. (2009a) for detailed vegetation, invertebrate and bird sampling techniques.

Stable isotope analysis

Stable N- and C- isotopic compositions of feather, invertebrate and plant samples were determined using a Thermo-Finnigan Delta Plus XP isotope ratio mass spectrometer configured on-line with a Costech ECS4010 elemental analyzer at the Stable Isotope Research Facility, Department of Geological Sciences, Indiana University, Bloomington, using methods outlined in Brittain et al. (2009a). Measured $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios are expressed as $\delta^{13}C$ and $\delta^{15}N$ values in ‰ relative to V-PDB and air nitrogen. We use the common delta notation:

$\delta X = (R_{sample}/R_{standard} - 1)*1000$,

where X = the element of interest (e.g., C or N) and R = the ratio of the heavier isotope to the lighter isotope of element X (e.g., $^{13}C/^{12}C$ or $^{15}N/^{14}N$). Instrument error was estimated by the standard deviation of acetanilide $\delta^{13}C$ (relative to VPDB) and $\delta^{15}N$ (relative to air), which averaged 0.06‰ and 0.16‰, respectively.

Statistics

Plants were grouped by photosynthetic pathway (C_3, C_4 or CAM) in each habitat, tested for differences using Multi-Response Permutation Procedures in PC-ORD 5.0 (McCune and Mefford 2006), and combined with other habitats until the isotopic signature of each group was different from the others (McCune and Grace 2002; Table 1). Invertebrates were grouped by feeding guild (according to Bland and Jacque 1978 and Kaston 1978) within each habitat and analyzed for differences using the same MRPP procedure as the plants (Table 2). Invertebrate families that only included species in either the carnivore, parasite, herbivore, detritivore or fungivore feeding guild were grouped into their respective guild, and the omnivore feeding guild was composed of families that were known omnivores or whose species represented more than one feeding guild. Bird feather isotopic values were grouped by species, habitat and age, and tested for differences using MRPP procedures but with additional sequential-Bonferroni corrections to preserve 5% experimental error and a conservative distinction between avian species (Holm 1979; Table 3). The standard errors of isotopic samples were propagated with the instrument error.

Source mixing models

Isosource 1.3.1 (available at: http://www.epa.gov/wed/pages/models/stableIsotopes/isosource/isosource.htm) was used to estimate the percent contribution of each potential primary producer source to the food web of each different avian habitat/age group using varying $\delta^{13}C$-enrichment steps and trophic levels to determine the range of possible solutions and sensitivity to model parameters as outlined in Brittain et al. (2009a). Mixing models were based on six potential sources for Sapelo Island and the three sources for Clayhole Swamp identified using MRPP. A matrix of nine potential models was run in *Isosource* for each species based on three different trophic levels and three ^{13}C-

enrichment rates (+2.5‰, +3.0‰ or +4.0‰). ^{15}N-enrichment was not varied from model to model due to the narrow range of differences seen by Pearson et al. (2003). Mean percent source results of all successful models were averaged to determine the likely source partitioning for each species (hereafter, mean results), and the standard deviations were propagated to assess variability.

The percent contribution of potential invertebrate and plant sources that may have been eaten directly by the birds were also modeled for all species except Eastern Screech Owl (no mammals or reptiles were sampled) using *Isosource* and similar techniques as primary production models detailed in Brittain et al. (2009a). *Isosource* sensitivity analysis of prey partitioning had nine models for each species with feather ^{13}C-enriched by either +2.5‰, +3.5‰ or +4.5‰, and ^{15}N-enriched at the same three rates, except for the saltmarsh species (Clapper Rail and Marsh Wren) which were ^{13}C-enriched by +0.5‰, +1.0‰ or +2.0‰ due to lack of successful models using the previously assumed enrichment levels.

RESULTS

Plant and invertebrate groups

Primary production of the three terrestrial and one saltmarsh habitats consisted of C_3 berries, C_3 leaves, C_3 saltmarsh vegetation, C_4 grasses, C_4 saltmarsh vegetation and CAM plants. In tidal forest, primary production groups consisted of bald cypress, herbaceous vegetation and other vegetation (Table 1). Detailed results of plant, invertebrate and bird analyses can be found in Brittain et al. (2009a).

Invertebrates were grouped into three isotopically unique guilds in each habitat based on Bland and Jacques (1978): carnivores/parasites/omnivores (CPO), detritivores (D) and herbivores/fungivores (HF). The CPO included araneae, coleoptera (cleridae and coccinellidae), diptera (dolichopodidae), hemiptera (reduviidae), hymenoptera (braconidae, eurytomidae, formicidae (classified as omnivores), sphecidae and tiphiidae) and mantidae. Detritivores were composed of blattaria, diplopoda, diptera (bibioniidae, culicidae and tipulidae), decapoda (*Uca pugnax*) and psocidae. The HF group comprised the most variety of taxa; acarina, coleoptera (alleculidae, buprestidae, chrysomelidae, ciidae, curculionidae, elateridae, mordellidae and phalacridae), diptera (tephritidae), hemiptera (alydidae, aphididae, cercopidae, cicadellidae, cixiidae, delphacidae, flatidae, lygeaidae, miridae, ortheziidae and pentatomidae), lepidoptera, littorinidae (*Littoraria irrorata*), orthoptera and thysanoptera.

Isoscapes

Plant groups from the C_3 photosynthetic pathway on Sapelo Island were depleted in ^{13}C (-27.51‰ for berries, -29.74‰ for terrestrial leaves and -26.84‰ for C_3 saltmarsh vegetation) relative to those from the CAM (-16.08‰) and C_4 pathways (-13.46‰ for C_4 terrestrial grasses and -13.92‰ for C_4 saltmarsh vegetation; Figure 2). However, both C_3 and C_4 saltmarsh vegetation groups were enriched in ^{15}N with positive values (1.8‰ and 5.6‰, respectively), whereas all terrestrial vegetation groups were depleted in ^{15}N with negative values (-2.2‰ for berries, -1.5‰ for leaves, -5.9‰ for CAM plants and -2.4‰ for C_4 terrestrial grasses). Saltmarsh invertebrate guilds were isotopically enriched in ^{13}C at a level similar to C_4 vegetation (-14.02‰ for HF to -16.32‰ for detritivores), but δ^{15}N values were highest for carnivores/parasites/omnivores (9.8‰) with decreasing values for herbivores/fungivores (8.1‰) and detritivores (4.4‰), respectively (Figure 2). Similarly, for the terrestrial habitats, CPO were ^{15}N-enriched (3.6 - 5.3‰) with decreasing δ^{15}N values for herbivores/fungivores (0.8 - 3.2‰) and detritivores (-1.4 - 3.7‰). In tidal forests, composed entirely of C_3 vegetation, herbaceous plants were the most ^{13}C-depleted (-33.59‰) and bald cypress was the most ^{13}C-enriched (-30.56‰) while “other” vegetation was depleted in ^{15}N (1.0‰ vs. 2.6‰ for herbaceous plants and

3.0‰ for cypress; Figure 3). Like saltmarsh vegetation, the tidal forest plant groups had positive $\delta^{15}N$ values. While CPO $\delta^{15}N$ values were highest among invertebrate groups in tidal forest (5.3‰), the herbivores/fungivore and detritivore groups had similar $\delta^{15}N$ values between them (3.2‰ and 3.7‰, respectively). Detritivores and CPO also had similar $\delta^{13}C$ values in tidal forest (-27.26‰ and –27.60‰, respectively).

Most terrestrial bird species had similar isotope signatures (Figure 2), but $\delta^{15}N$ values of Eastern Screech Owls (7.4‰), Carolina Wrens (7.2‰) and Red-bellied Woodpeckers (6.8‰) were more positive than those in other terrestrial bird species (4.4‰ for after-hatch-year Yellow-throated Warblers to 6.5‰ for young-of-year White-eyed Vireos). Painted Buntings were more ^{13}C-enriched (-14.87‰), as were Clapper Rails (-14.04‰) and Marsh Wrens (-14.23‰). Carolina Wrens and Northern Parula were greatly enriched in both ^{13}C and ^{15}N isotopes (by ~6‰) relative to tidal forest vegetation (Figure 3). Generally, isoscapes showed that feathers were ^{13}C and ^{15}N-enriched compared to plants and that Painted Buntings were the only terrestrial species isotopically similar to saltmarsh vegetation (Figure 2 and 3).

Primary production source mixing models

No models of primary production supplying the base of the food web in tidal forest were successful. Within the saltmarsh on Sapelo Island, C_4 saltmarsh vegetation (*Spartina alterniflora*) supplied 33-64% the primary production to Clapper Rail food webs (Table 4) and 31-48% to Marsh Wren food webs. Conversely, the proportion of C_3 saltmarsh vegetation in avian food webs was 0-57% for Clapper Rails and 30-66% for Marsh Wrens.

In pine forest habitats, C_3 leaves from terrestrial vegetation provided approximately 20-93% of the primary production in the food webs of Red-bellied Woodpeckers and 10-92% of Brown-headed Nuthatch food webs (Table 4). In shrub habitat, Brown-headed Nuthatch food webs were comprised of 14-80% C_3 leaves. However, while model results indicate that Brown-headed Nuthatches in pine forest had 0-43% of their food web originate from C_3 saltmarsh vegetation, those in shrub habitat had 11-72% from C_3 saltmarsh.

Across the three terrestrial habitats, C_3 leaves provided the bulk of the base of the food webs of most avian species (42-92% for Eastern Screech Owl, 21-92% for young-of-year White-eyed Vireo, 40-87% for after-hatch-year White-eyed Vireo, 14-89% for Carolina Wren, 41-89% for Northern Parula, 18-87% for young-of-year Yellow-throated Warbler, and 38-95% for after-hatch-year Yellow-throated Warbler; Table 4). However, Painted Bunting food webs had smaller inputs from C_3 leaves (0-42%).

Berries only provided more substantial portions of the food web production for adult Brown-headed Nuthatches from pine forest (up to 68%; Table 4). CAM plants, C_4 saltmarsh vegetation and C_4 terrestrial grasses were relatively insignificant contributors of primary production to terrestrial avian food webs (less than 12%), except Painted Buntings (up to 39%, 46% and 50%, respectively).

C_3 saltmarsh vegetation, which grows at the ecotone between the saltmarsh and terrestrial forests, often provided the second highest amount of primary production in avian food webs for species in terrestrial and saltmarsh habitats, but its contribution was highly variable (Table 4). Brown-headed Nuthatches in pine forest had 0- 43% of their food web based upon C_3 saltmarsh vegetation, whereas nuthatches in shrub habitat had 11-72%. Similarly, young-of-year White-eyed Vireo food webs were 0-66% based on C_3 saltmarsh production, but after-hatch-year vireos had 6-48%. Young-of-year Yellow-throated Warblers also had 0-60% of their food webs based on C3 saltmarsh production, whereas the after-hatch-year warblers had 1-21%. Painted Buntings received up to 51% of their food web from C_3 saltmarsh production.

Invertebrate source mixing models

Carolina Wrens in tidal forest fed most heavily on CPO (22-100%), with only 17-28% contributing from HF (Table 5). Conversely, Northern Parula in tidal forest ate more evenly from all three invertebrate guilds. Tidal forest CPO included spiders, Braconidae, Formicidae, Mantodea and Dolichopodidae, detritivores included Diplopods and Tipulidae, and HF were a blend of various Coleoptera, Hemiptera, Lepidoptera and Orthoptera.

In saltmarsh habitat, Clapper Rails preyed upon the three invertebrate guilds fairly evenly (6-50% from CPO, 18-53% from detritivores, and 8-64% from HF; Table 5), but Marsh Wrens ate more CPO (50-86%). Saltmarsh detritivores were exclusively fiddler crabs, and CPO was made up of spiders, Cleridae and Formicidae.

In pine forests, Red-bellied Woodpeckers preyed upon CPO invertebrates most heavily (66-72%; Table 5). Young-of-year Brown-headed Nuthatch prey items in pine forest were also dominated by CPO invertebrates (24-89%), but after-hatch-year nuthatch CPO prey were only 3-64%. Models also indicate that Brown-headed Nuthatches in pine forest ate only less than 10% pine vegetation. Nuthatches incidentally caught in shrub habitat ate more evenly from the three invertebrate guilds and pine vegetation than those captured in pine forest. Pine forest CPO were dominated by spiders, Formicidae and Braconidae, detritivores were exclusively Psocidae, and HF were composed mainly of Hemiptera, Lepidoptera and Orthoptera.

Dominant avian food items varied among species in terrestrial habitats, but CPO, mainly spiders, appeared to be the favored foraging guild (Table 5). Painted Bunting models show they were eating a combination of C_4 grasses (5-42%), saltmarsh HF (0-65%) and saltmarsh CPO (0-49%), with lesser amounts from terrestrial sources. Northern Parula consumed primarily oak and pine forest CPO (12-78%). Like their tidal forest counterparts, Carolina Wrens in terrestrial habitats were eating CPO not only from oak and pine forest (6-69%), but also shrub habitat (7-58%). Young-of-year Yellow-throated Warblers ate 16-71% oak and pine CPO and after-hatch-year warblers ate 0-51%. Similarly, young-of-year Yellow-throated Warblers consumed 0-27% oak detritivores, but after-hatch-year warblers consumed 7-56%. Young-of-year and after-hatch-year White-eyed Vireos ate prey sources in relatively similar proportions, but were dominated by oak and pine forest CPO (33-73% and 20-75%, respectively). However, young-of-year White-eyed Vireo diets were 0-24% berries while after-hatch-year vireos ate 0-38%. Terrestrial Sapelo Island detritivores were mostly Psocidae with a few Bibionidae and Blattaria, and HF were a blend of various Coleoptera, Hemiptera, Lepidoptera and Orthoptera.

DISCUSSION

Isosource mixing models

Isosource operates by giving the frequency, range, mean and standard deviation of the percent of each potential source in the species' diet for all solutions that satisfy the mass balance between them, giving a broad picture of source partitions (Phillips and Gregg 2003). Without knowing the exact trophic levels and feather $\delta^{13}C$ or $\delta^{15}N$ trophic increases from each species in their given habitat, there is no way to determine which model was actually the most accurate, but the mean of the successful model results, ± propagated standard deviations, represents our least biased estimate of the relative proportions of each potential food source (Brittain et al. 2009a). The lack of successful primary production source models in the tidal forest where all vegetation utilized the C_3 photosynthetic pathway and was subjected to the same hydrologic conditions suggests that researchers will need vegetation from different photosynthetic pathways to separate $\delta^{13}C$, or different hydrologic regimes to separate $\delta^{15}N$ in order to model proportional contributions of potential primary production sources to food webs.

Primary production sources

The range of model results for both Marsh Wrens and Clapper Rails suggests their food webs are heavily dependent on vegetation originating from the saltmarsh, but wrens receive more from the C_3 saltmarsh vegetation in the ecotone between the saltmarsh and terrestrial habitats than rails. Although most terrestrial species were highly dependent on C_3 leaf production from the habitats they occupied, birds captured in the narrow shrub habitat zone between terrestrial forests and saltmarsh or dunes, including Carolina Wrens, White-eyed Vireos and Brown-headed Nuthatches, showed a greater reliance on food webs originating from the C_3 saltmarsh pathway. However, Painted Buntings relied more on production from the low saltmarsh C_4 vegetation than any other terrestrial species. Young White-eyed Vireos and Brown-headed Nuthatches also derived more food from the saltmarsh-shrub ecotone than adults of the same species. The dependence on saltmarsh vegetation by shrub-associated species suggests that they may not be feeding in the shrub habitat where researchers typically see them, or that airborne invertebrates are transferring carbon and nutrients from one habitat to another. The increased production of C_3 saltmarsh vegetation in young-of-year birds indicates a potential early breeding season source of protein in the saltmarsh-shrub ecotone during the nestling phase. The relatively equal proportions of primary production sources in Painted Bunting food webs, and higher variability in their isotopic composition, supports the assumption of greater variability with a wide range of prey items (Bearhop et al. 2004).

Invertebrate sources

Invertebrate sources for both saltmarsh species, Clapper Rail and Marsh Wren, could not be partitioned successfully at the expected 2.5‰ to 4.5‰ ^{13}C-enrichment levels and were only successful with 0.5‰ to 1.5‰ enrichment. The lack of consistency in ^{13}C-enrichment levels between saltmarsh and other species indicates that trophic δ^{13}C increases may differ between saltmarsh and terrestrial habitats. Lower propagated standard deviations suggest that Clapper

Rails ate more detritivores, comprised primarily of *Uca pugnax*, agreeing with other studies in the region (Oney 1951, Meanley 1985). Marsh Wrens ate more CPO, presumably the Araneae and Hymenoptera typical of their diets (Kale 1964). Marsh Wrens were captured exclusively in C_4 *Spartina alterniflora*, indicating that although they occupy C_4 saltmarsh zones, a large portion of their food comes from C_3 saltmarsh-shrub ecotone.

Models indicate that oak and pine forest CPO was the most frequently consumed invertebrate guild among the birds in coastal terrestrial habitats. Northern Parula in tidal forest, however, ate more detritivores, likely due to the abundance of dipteral food sources in these forested wetlands (Stevenson and Anderson 1994). Adult Yellow-throated Warblers ate many shrub and pine forest detritivores, possibly Psocoptera and Bibionidae (love bugs) common in these habitats. Painted Buntings fed on C_4 grasses, HF and CPO, as reported in other studies (Beal et al. 1916, Howell 1932). However, Painted Bunting HF and CPO prey items appeared to come mostly from saltmarshes, presumably Orthoptera (*Orchelimum fidicinium*) and Delphacidae from HF, and Formicidae from CPO. White-eyed Vireos, Carolina Wrens, Red-bellied Woodpeckers and Brown-headed Nuthatches are all known to feed on the spiders, parasitic wasps, lady bug beetles, ants and long-legged flies (Dolichopodidae) that made up the oak and pine CPO group (Beal 1911, Beal et al. 1916, Norris 1958, Nolan and Wooldridge 1962).

Brown-headed Nuthatches and adult Yellow-throated Warblers were the only terrestrial species that models indicate preyed heavily on detritivores, presumably the Psocoptera and Blattaria as found by Norris (1958), but the saltmarsh and tidal forest birds also ate a large portion of detritivores. Saltmarsh detritivores were made up mostly of fiddler crabs, whereas Diplopods and Tipulidae were abundant in tidal forests. The high proportion of berries in adult White-eyed Vireo diets is consistent with Chapin (1925) and Nolan and Woolridge (1962).

Habitat Overlap

Many shrub birds and Marsh Wrens ate a large portion of prey that originated from C_3 saltmarsh vegetation outside of their associated habitats, suggesting that this saltmarsh-shrub ecotone is an important feeding habitat for some avian species. For example, the species of highest concern in the region, Painted Bunting (Hunter et al. 2001), appears to be almost as dependent on saltmarsh vegetation as shrub and forest vegetation where it was more commonly observed. The moderate levels of all six food web pathways in Painted Bunting diets indicate variable foraging on many sources of prey for this species (Hunter et al. 2001, Bearhop et al. 2004).

The mode of nutrient flow, birds foraging in saltmarsh vs. saltmarsh invertebrates moving to terrestrial habitat, is largely unknown. However, Marsh Wrens are likely feeding on spiders that prey upon flying insects (e.g., Diptera) that originated in the saltmarsh-shrub ecotone, while Painted Buntings are known to forage directly in the saltmarsh (Brittain et al. 2009b). The apparent added dependence of young-of-year birds on C_3 saltmarsh vegetation also indicates potential temporal variability in species' foraging habits. The saltmarsh-shrub ecotone, which occupies isolated linear patches comprising only 0.2% of the coastal Georgia landscape (Brittain et al. 2009c), may provide an important source of invertebrate protein during the period of nestling growth across coastal habitats. While birds that occupy shrub habitat may easily move to the saltmarsh-shrub ecotone to forage for nestling food, it is doubtful that Brown-headed Nuthatches and Yellow-throated Warblers captured deep in the forest foraged so far afield, rather the prey items likely came to them from the ecotone.

CONCLUSIONS

Saltmarsh and most terrestrial bird species appear to be highly trophically connected to their respective habitats. However, shrub-associated species, such as Painted Buntings and White-eyed Vireos, appear to be more dependent on saltmarsh vegetation than other terrestrial species. Painted Buntings appear to be foraging generalists, whereas Brown-headed Nuthatches and Yellow-throated Warblers likely take advantage of windfall prey. Marsh Wrens similarly appear take advantage of windfall prey arriving in C_4 saltmarsh zones near tidal creeks where they nest. C_3 saltmarsh vegetation from the saltmarsh-shrub ecotone appears to provide food for many terrestrial species at the critical nestling breeding phase. While carnivores/parasites/omnivores appear to be the most common prey items for terrestrial avian species, Northern Parula in tidal forest switched to detritivores as the dominant prey items. Conservation of shrub habitat in coastal Georgia for bird species, especially Painted Bunting, should include nearby saltmarsh in order to provide the necessary food resources at the appropriate time.

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TABLE 1. Isotopic signatures of primary production sources in coastal Georgia.

Location	Source	N	$\delta^{13}C$	$\delta^{15}N$
Oak & pine forest and shrub	C_3 berries	24	-27.51 ±0.09	-2.2 ±0.1
	C_3 leaves	66	-29.74 ±0.03	-1.5 ±0.0
	CAM plants	6	-16.08 ±0.14	-5.9 ±0.1
	C_4 grasses	5	-13.46 ±0.07	-2.4 ±0.2
Saltmarsh	C_3 saltmarsh	16	-26.84 ±0.11	1.8 ±0.2
	C_4 saltmarsh	8	-13.92 ±0.12	5.6 ±0.2
Tidal forest	Cypress	6	-30.56 ±0.28	3.0 ±0.3
	Herbs	9	-33.59 ±0.12	2.6 ±0.1
	Other	21	-31.91 ±0.04	1.0 ±0.1

Mean $\delta^{13}C$ (in ‰) and $\delta^{15}N$ (in ‰) ± 1 SE of pooled isotopic results. See Appendix 1 for individual species results. All groups within each habitat were significantly different between each other using Multi-Response Permutation Procedures ($\alpha = 0.05$).

TABLE 2. Isotopic signatures of invertebrate prey sources in coastal Georiga, grouped by feeding guild.

	Invertebrate Feeding Guild								
	Herbivores/Fungivores			Detritivores			Carnivores/Parasites/Omnivores		
Habitat	N	$\delta^{13}C$	$\delta^{15}N$	N	$\delta^{13}C$	$\delta^{15}N$	N	$\delta^{13}C$	$\delta^{15}N$
saltmarsh	33	-14.02 ±0.20	8.1 ±0.3	6	-16.32 ±0.50	4.4 ±0.4	13	-14.76 ±0.69	9.8 ±0.8
shrub	70	-24.40 ±0.46	1.8 ±0.2				44	-23.43 ±0.37	4.8 ±0.4
oak forest				9	-27.70 ±0.18	-1.4 ±0.2			
oak & pine forest	48	-26.27 ±0.51	0.8 ±0.3				51	-26.21 ±0.21	3.6 ±0.3
shrub & pine forest				17	-26.54 ±0.25	0.0 ±0.7			
tidal forest	55	-29.18 ±0.31	3.2 ±0.3	11	-27.26 ±0.34	3.7 ±0.6	44	-27.60 ±0.21	5.3 ±0.2
Contributing taxonomy	acarina, alleculide, alydidae, aphididae, buprestidae, cercopidae, chrysomelidae, cicadellidae, ciidae, cixiidae, curculionidae, delphacidae,			bibioniidae, blattaria, culicidae, diplopoda, ocypodidae, psocidae, tipulidae			araneae, braconidae, cleridae, coccinellidae, dolichopodidae, eurytomidae, formicidae, mantidae, reduviidae, sphecidae, tiphiidae		

	elateridae, flatidae, lepidoptera, littorinidae, lygaeidae, miridae, mordellidae, ortheziidae, orthoptera, pentatomidae, phalacridae, tephritidae, thysanoptera

Mean $\delta^{13}C$ (in ‰) and $\delta^{15}N$ (in ‰) ± 1 SE of pooled isotopic results. See Appendix 2 for taxonomic family results. All groups within each habitat were significantly different between each other using Multi-Response Permutation Procedures ($\alpha = 0.05$).

TABLE 3. Sample size (N), mean $\delta^{13}C$ (in ‰) and $\delta^{15}N$ (in ‰) ± 1 SE of bird feathers sampled in five habitats of coastal Georgia in 2006 and 2007. See text for scientific names of bird species. "AHY" = after-hatch-year birds and "YOY" = young-of-year birds. Standard errors have been additively propagated with the instrument error.

Habitat	Species	Age	N	$\delta^{13}C$	$\delta^{15}N$
Saltmarsh	Clapper Rail	all	4	-14.04 ±0.78	10.6 ±0.6
	Marsh Wren	all	18	-14.23 ±0.89	12.9 ±0.3
Pine forest	Red-bellied Woodpecker	all	12	-22.30 ±0.13	6.8 ±0.2
	Brown-headed Nuthatch	all*	51	-22.20 ±0.09	5.2 ±0.1
		YOY*	22	-22.33 ±0.09	5.6 ±0.2
		AHY*	22	-22.11 ±0.17	4.9 ±0.2
Shrub	Brown-headed Nuthatch	all*	5	-22.76 ±0.37	4.9 ±0.4
Sapelo Island	Eastern Screech Owl	all	27	-22.43 ±0.16	7.4 ±0.2
	White-eyed Vireo	YOY*	22	-23.28 ±0.19	6.5 ±0.2
		AHY*	23	-23.76 ±0.23	5.5 ±0.2
	Carolina Wren	all*	21	-21.93 ±0.29	7.2 ±0.2
	Northern Parula	all*	66	-23.75 ±0.07	5.4 ±0.2

	Yellow-throated Warbler	YOY*	12	-22.92 ±0.10	6.1 ±0.3
		AHY*	11	-23.27 ±0.15	4.4 ±0.3
	Painted Bunting	all	40	-14.87 ±0.65	6.7 ±0.4
Tidal forest	Carolina Wren	all*	13	-24.35 ±0.21	7.6 ±0.3
	Northern Parula	all*	23	-23.95 ±0.12	7.3 ±0.4

* indicates isotopic results that are different between habitats or ages for each species based on Multi Response Permutation Procedures, corrected using sequential Bonferroni methods ($\alpha = 0.05$).

Mean $\delta^{13}C$ (in ‰) and $\delta^{15}N$ (in ‰) ± 1 SE results of feathers. See text for scientific names of bird species. “AHY” = after-hatch-year birds. Standard errors have been additively propagated with the instrument error.

TABLE 4. Average model results, ± propagated standard deviations, of primary production sources at the base of avian food webs in coastal Georgia from Brittain et al. (2009a). Models run for each species varied the trophic steps (2.0 – 4.0 at 0.5 intervals) with either +2.5‰, +3.5‰ or +4.5‰ $\delta^{13}C$ enrichment in the feathers at each trophic step. "Sapelo Island" habitat results are for data pooled across shrub, oak forest and pine forest. Sources: "C3B" = C_3 berries, "C3L" = C_3 leaves, "C3S" = C_3 saltmarsh vegetation, "C4G" = C_4 grasses, "C4S" = *Spartina alterniflora*, and "CAM" = CAM plants. "AHY" = after-hatch-year birds and "YOY" = young-of-year birds.

			Primary Production Sources					
Habitat	Species	Age	C3B	C3L	C3S	C4G	C4S	CAM
Saltmarsh	Clapper Rail	all	7.7 ±20.5	13.5 ±26.7	27.5 ±29.7	4.0 ±10.6	48.3 ±15.6	2.8 ±7.9
	Marsh Wren	all	3.9 ±6.5	6.4 ±10.1	47.7 ±17.8	1.6 ±3.1	39.5 ±8.4	1.1 ±2.3
Pine forest	Red-bellied Woodpecker	all	14.0 ±32.6	56.7 ±36.4	24.0 ±24.9	1.2 ±3.6	2.0 ±5.5	2.2 ±5.5
	Brown-headed Nuthatch	all	20.1 ±38.0	51.1 ±41.0	19.2 ±24.2	3.0 ±7.0	3.3 ±7.7	3.3 ±7.0
	Brown-headed Nuthatch	YOY	18.0 ±41.9	49.1 ±43.0	25.2 ±27.5	1.9 ±5.5	2.8 ±7.6	3.0 ±7.4
	Brown-headed Nuthatch	AHY	24.9 ±43.7	50.9 ±43.3	14.0 ±21.8	3.1 ±7.1	3.0 ±7.2	4.2 ±8.1
Shrub	Brown-headed Nuthatch	all	7.9 ±16.9	46.7 ±32.8	41.3 ±30.6	1.1 ±2.9	2.1 ±4.6	1.0 ±2.8
Sapelo Island	Eastern Screech Owl	all	11.3 ±20.0	67.0 ±25.1	17.6 ±19.0	1.3 ±3.1	1.5 ±3.6	1.5 ±3.1
	White-eyed Vireo	YOY	7.6 ±13.9	56.6 ±35.3	32.6 ±33.4	0.9 ±2.3	1.5 ±3.2	0.9 ±2.2
	White-eyed Vireo	AHY	6.8 ±14.5	63.8 ±23.9	26.5 ±21.0	0.8 ±2.3	1.4 ±3.3	0.8 ±2.3
	Carolina Wren	all	13.7 ±31.6	51.7 ±37.8	28.9 ±28.7	1.6 ±4.7	2.1 ±6.4	2.0 ±5.3

Northern Parula	all	7.9 ±15.8	65.1 ±24.3	2.7 ±20.7	0.9 ±2.5	1.5 ±3.4	1.0 ±2.5
Yellow-throated Warbler	YOY	12.5 ±26.1	52.6 ±34.3	30.2 ±29.9	1.3 ±3.7	1.8 ±5.2	1.7 ±4.3
Yellow-throated Warbler	AHY	15.5 ±24.4	66.8 ±28.4	11.1 ±10.3	2.1 ±4.1	2.4 ±3.7	2.2 ±4.0
Painted Bunting	all	14.4 ±32.9	13.2 ±29.3	16.7 ±34.7	17.7 ±32.4	24.9 ±21.1	13.2 ±25.7

TABLE 5. Average model results, ± propagated standard deviations, of direct avian prey sources in coastal Georgia from Brittain et al. 2009a. Models run for each species had either +2.5‰, +3.5‰ or +4.5‰ $\delta^{13}C$ increase, and +2.5‰, +3.5‰ or +4.5‰ $\delta^{15}N$ increase in the feathers for one trophic step. "Sapelo Is." habitat results are for data pooled across shrub, oak forest and pine forest. Sources: "CPO" = carnivores, parasites and omnivores, "Det" = detritivores, "HF" = herbivores and fungivores, "op" = coming from oak and pine forests, "o" = coming from oak forest only, "sh" = coming from shrub only, "shp" = coming from shrub and pine forest, and "sa" = coming from saltmarsh. "AHY" = after-hatch-year birds and "YOY" = young-of-year birds.

			Invertebrate and Plant Sources						
Habitat	Species	Age	CPO	Det	HF				
saltmarsh	Clapper Rail	all	28.1 ±21.8	35.6 ±17.9	36.3 ±28.1				
	Marsh Wren	all	67.6 ±18.1	15.4 ±11.4	17.0 ±18.7				
			CPO	Det	HF	C3L	C3B		
pine forest	Red-bellied Woodpecker	all	68.7 ±3.2	8.9 ±6.0	10.8 ±7.2	5.0 ±2.9	6.6 ±4.6		
	Brown-headed Nuthatch	all	41.3 ±32.8	25.4 ±31.4	28.5 ±36.2	4.9 ±2.0			
	Brown-headed Nuthatch	YOY	56.4 ±32.5	16.1 ±25.4	19.6 ±30.8	7.9 ±1.8			
	Brown-headed Nuthatch	AHY	33.5 ±30.2	36.4 ±35.8	26.4 ±29.8	3.8 ±2.2			
shrub	Brown-headed Nuthatch	all	27.5 ±25.2	28.5 ±39.5	24.2 ±38.0	19.9 ±14.5			
			sh CPO	shp Det	sh HF	sa CPO	sa HF	C3B	C4G

Sapelo Is.	Painted Bunting	all	10.1 ±25.3	8.5 ±21.0	9.9 ±24.7	17.0 ±32.1	23.8 ±41.4	7.2 ±17.5	23.6 ±18.7
			op CPO	o Det	op HF	sh CPO	shp Det	sh HF	
	Northern Parula	all	44.9 ±33.1	14.5 ±18.1	15.6 ±25.4	5.3 ±8.4	14.4 ±22.7	5.4 ±8.8	
	Yellow-throated Warbler	YOY	43.4 ±27.7	11.1 ±16.1	10.2 ±21.3	15.3 ±18.4	9.8 ±20.6	10.2 ±19.9	
	Yellow-throated Warbler	AHY	25.0 ±25.8	31.3 ±24.7	11.6 ±23.8	6.0 ±12.4	14.4 ±28.6	11.8 ±19.2	
			op CPO	op HF	sh CPO	shp Det	sh HF	C3B	
	White-eyed Vireo	YOY	52.8 ±20.2	9.5 ±16.3	10.7 ±12.3	7.9 ±13.3	7.3 ±12.2	11.7 ±12.6	
	White-eyed Vireo	AHY	47.7 ±27.4	12.2 ±24.8	4.5 ±8.8	11.2 ±22.0	6.3 ±11.9	18.2 ±19.6	
	Carolina Wren	all	37.7 ±31.2	6.3 ±13.2	32.8 ±25.0	5.3 ±11.2	13.1 ±21.6	4.9 ±8.6	
			CPO	Det	HF				
tidal forest	Carolina Wren	all	61.1 ±39.2	21.2±29.4	17.7 ±10.3				
	Northern Parula	all	31.7 ±32.7	45.5 ±35.4	22.8 ±31.2				

FIG. 1. Map of study area on Sapelo Island, McIntosh County, Georgia and location of bird banding sites in saltmarsh, maritime scrub-shrub, maritime broadleaf evergreen forest and maritime narrowleaf evergreen forest.

FIG. 2. Isoscape of $\delta^{13}C$ and $\delta^{15}N$ values (± SE bars) for plants, invertebrate feeding groups and birds sampled on Sapelo Island, Georgia in 2006-2007. CLRA = Clapper Rail, EASO = Eastern Screech Owl, RBWO = Red-bellied Woodpecker, WEVI = White-eyed Vireo, BHNU = Brown-headed Nuthatch, CARW = Carolina Wren, MAWR = Marsh Wren, NOPA = Northern Parula, YTWA = Yellow-throated Warbler and PABU = Painted Bunting. "opC" = carnivores, parasites and omnivores from oak and pine forests, "oD" = detritivores from oak forest, "opH" = herbivores and fungivores from oak and pine forests, "shC" = carnivores, parasites and omnivores from shrub habitat, "shpD" = detritivores from shrub and pine forest, "shH" = herbivores and fungivores from shrub habitat, "saC" = carnivores, parasites and omnivores from saltmarsh, "saD" = detritivores from saltmarsh, and "saH" = herbivores and fungivores from saltmarsh.

FIG.3. Isoscape of $\delta^{13}C$ and $\delta^{15}N$ values (± SE bars) for plants, invertebrate feeding groups and birds sampled in Clayhole Swamp, Georgia in 2006-2007. CARW = Carolina Wren and NOPA = Northern Parula. "C" = carnivores, parasites and omnivores, "D" = detritivores, and "H" = herbivores and fungivores from tidal forests.

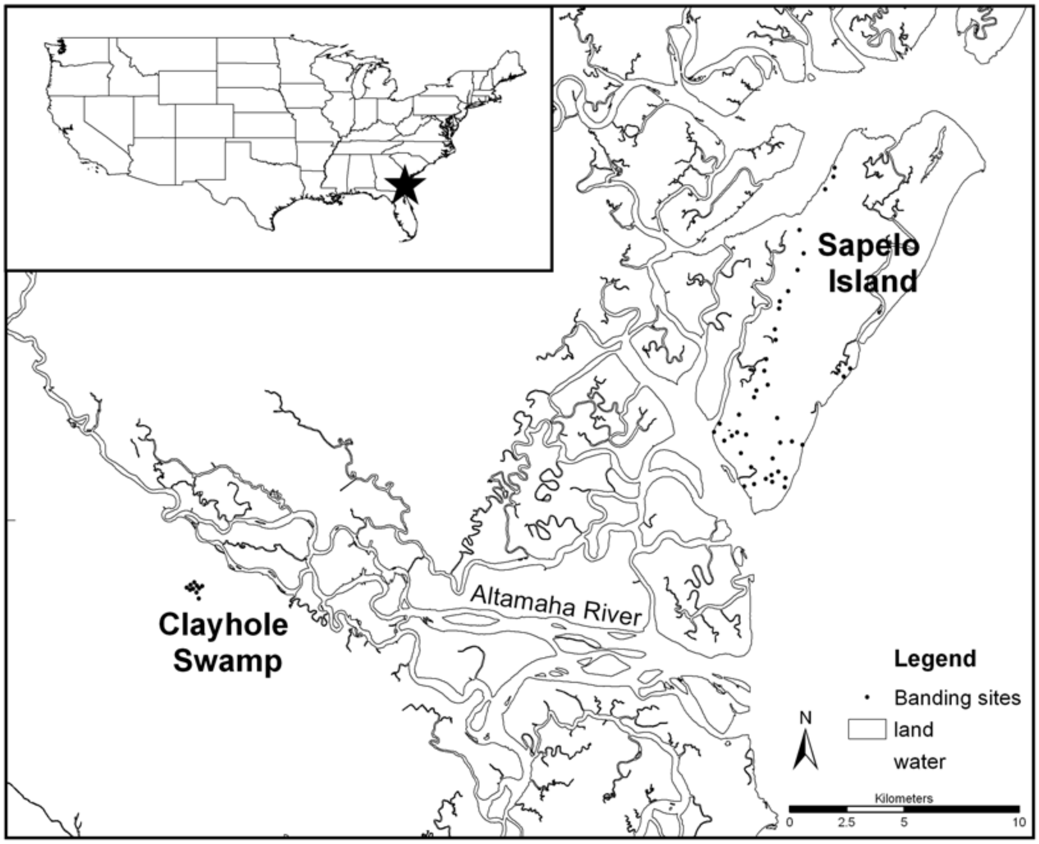
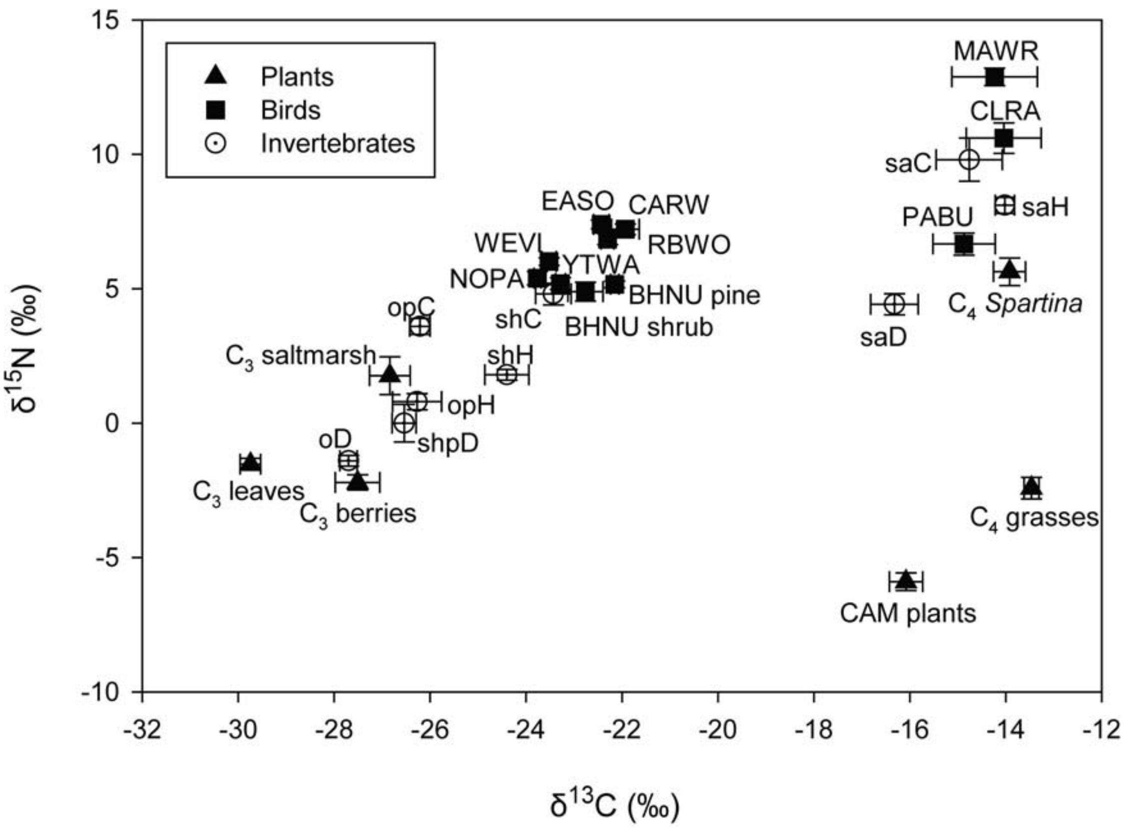

Sapelo
Island
Clayhole
Swamp
Altamaha River
Legend
Banding sites
land
water
N
Kilometers
0
2.5
5
10

Figure 1.



Plants
Birds
Invertebrates
MAWR
CLRA
saC
saH
PABU
C4 Spartina
saD
EASO
CARW
RBWO
WEVI
YTWA
NOPA
BHNU pine
BHNU shrub
shC
opC
shH
C3 saltmarsh
opH
shpD
oD
C3 leaves
C3 berries
C4 grasses
CAM plants
δ15N (‰)
δ13C (‰)
15
10
5
0
-5
-10
-32
-30
-28
-26
-24
-22
-20
-18
-16
-14
-12

Figure 2.

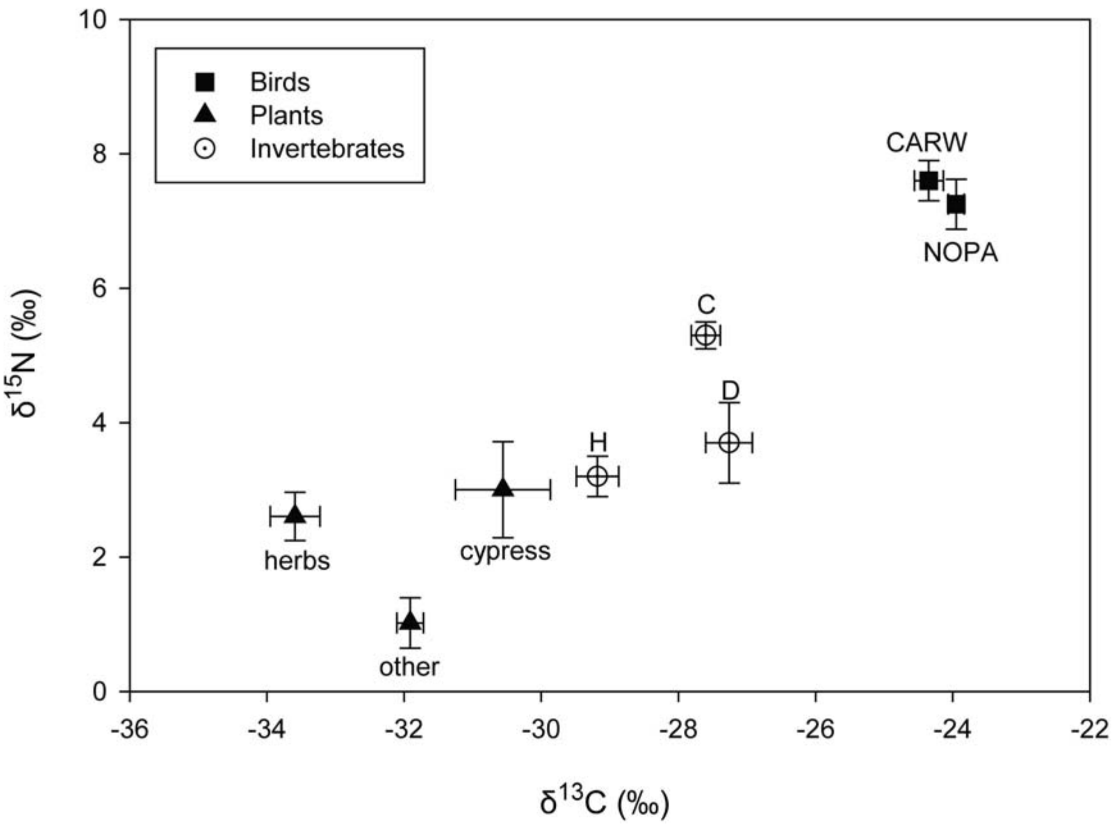

10
8
6
4
2
0
Birds
Plants
Invertebrates
CARW
NOPA
C
D
H
herbs
cypress
other
-36
-34
-32
-30
-28
-26
-24
-22
δ15N (‰)
δ13C (‰)

Figure 3.

STEMMING THE TIDE?

PREDICTING THE EFFECTS OF SEA-LEVEL RISE AND ANTHROPOGENIC DEVELOPMENT ON AVIAN PRIORITY SPECIES IN COASTAL GEORGIA, USA.

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Abstract. We modeled the loss of five habitats (tidal-freshwater forest, saltmarsh, maritime shrub-scrub, maritime broadleaf forest and maritime narrowleaf forest) in coastal Georgia, USA, due to sea-level rise (SLR) and urban development for 2100 since these are the major contributors to habitat loss in the region. Development rates, based on regional growth plans, were modeled at 1% and 2.5% annual urban growth, while SLR rates, based on the Intergovernmental Panel on Climate Change's A1B mean and maximum scenarios, were modeled at 52 cm and 82 cm, respectively. Saltmarsh, tidal forest and maritime shrub habitats are under greater threat from SLR than development, due to their proximity to the ocean, with up to 45%, 35% and 44% losses, respectively by 2100. Urban development threatens oak and pine forests, especially under 2.5% annual growth development scenarios, but pine forest loss is greatest from SLR when annual development rates were 1%.

Due to its small area and threats from both development and SLR, shrub habitat preservation efforts are recommended. Resource managers will need to maintain suitable open-canopy oak and pine forests as refuge for shrub-associated species, such as Painted Buntings, as shrub habitat disappears. Tidal forests may serve as refuges for closed-canopy species, such as Northern Parula and Acadian Flycatcher, that lose appropriate oak and pine forests to development. An adaptive management approach is recommended that monitors SLR and development rates in coastal Georgia, shifting from efforts focused on protecting pine forest and shrub habitat with moderate development rates to protecting oak forest and shrub with accelerated development.

Keywords: GIS, sea-level rise, development, avian conservation, habitat, Georgia

INTRODUCTION

Populations of most migratory birds have declined in recent decades despite recognition of the important ecosystem services they provide such as seed dispersal, pollination and insect control (Kirk et al. 1996, Price and Root 2001, Rosenstock et al. 2002). Habitat loss, isolation and fragmentation are considered the greatest threats to avian conservation (van Dyke 2003). Factors important to bird distributions across a landscape include habitat, food availability and climate (Price and Root 2001), but wildlife managers also need accurate population estimates to maintain viable avian populations (Buckland et al. 2001).

The south Atlantic coastal plain physiographic area covers about 101,000 km^2 in parts of six states from Virginia to Alabama, has over 160 breeding bird species, contains the largest forested floodplains outside the Mississippi Alluvial Plain in North America, and has the "best remaining examples of 'natural' barrier and sea islands and maritime forests in the southeast" (Hunter et al. 2001). However, 40% of natural vegetation has been lost due to land conversion (Hunter et al. 2001).

Coastal development and sea-level rise (SLR) are major threats contributing to habitat loss in the region (NOAA 2003, Craft et al. 2009). Georgia's coastal population is growing approximately 20% per decade, with concurrent anthropogenic development and habitat loss (NOAA 2003). Simultaneously, sea-level is predicted to rise 30-100 cm by 2100 (Meehl et al. 2007), leading to loss of saltmarshes, tidal swamp forests and coastal terrestrial habitats (Craft et al. 2009). Partners In Flight's (PIF) conservation issues within the region include management and conservation of forested floodplains, and protection of vulnerable neotropical migratory landbirds through habitat maintenance (Hunter et al. 2001). Georgia's Coastal Management Program goals also include attracting and sustaining historic migratory bird populations, and maintaining viable wildlife populations (NOAA 2003).

Within the south Atlantic coastal plain, PIF recognizes five bird-habitat associations of importance: 1) early successional shrub-scrub maintained by frequent and large-scale disturbance regimes, such as fire, 2) southern pine dominated by loblolly (*Pinus taeda*), slash (*Pinus elliottii*) and longleaf pine (*Pinus palustris*) with frequent fires, 3) forested wetlands dominated by bald cypress (*Taxodium distichum*) and water tupelo (*Nyssa aquatica*), 4) maritime woodlands dominated by live oak (*Quercus virginiana*), and 5) estuarine emergent wetlands such as saltmarsh (Hunter et al. 2001).

The conservation importance rank of any PIF species should include both the population densities within each habitat and the relative abundance of the habitat (New 1997, Balcombe et al. 2005). Habitat abundance changes over time due to anthropogenic and natural processes of land conversion. Thus, resource managers need to assess the combined effects of development and SLR on habitat in coastal areas.

We used breeding bird densities, simulation modeling of SLR and urban development, and species-habitat associations used in Gap analysis (Gap analysis is used to identify gaps between preserved habitats by comparing the modeled distribution of a species based on vegetation types with the distribution of preserved landscapes in GIS; Scott et al. 1993) to predict changes in habitat and breeding bird populations in the coming century in habitats of coastal Georgia. Our efforts focused on five habitats (maritime scrub-shrub, maritime narrowleaf evergreen forest, tidal-freshwater broadleaf deciduous forest, maritime broadleaf evergreen forest, and emergent saltmarsh) to evaluate avian susceptibility to habitat loss caused by both anthropogenic (development) and natural (SLR) disturbances. We estimate avian breeding populations of PIF priority species in each habitat using breeding bird densities and GIS estimates of land cover area. The effects of sea-level rise and urban development on habitat availability and avian populations are modeled for the year 2100, using breeding bird densities based on distance-sampling methods (Brittain et al. 2009a), 1% and 2.5% annual rates of development (NOAA 2003) and simulations of accelerated SLR for the region based on the Intergovernmental Panel on Climate Change (IPCC) A1B mean and maximum scenarios (Craft et al. 2009). The conservation implications of these predicted changes are discussed.

METHODS

Site description and field sampling

Tidal-freshwater broadleaf deciduous forest (tidal forest), saltmarsh, maritime scrub-shrub (shrub), maritime broadleaf evergreen forest (oak forest), and maritime narrowleaf evergreen forest (pine forest) were surveyed for breeding birds. Tidal forest was located in the Clayhole Swamp Wildlife Management Area on the Altamaha River in Glynn County, Georgia, owned and managed by the Georgia Department of Natural Resources. The other four habitats were all located on the 6,677 hectare (hectare = 10,000 m^2) Sapelo Island, McIntosh County, Georgia, on property jointly owned and managed by the Georgia Department of Natural Resources and the Sapelo Island National Estuarine Research Reserve. For details on the exact location of sampling sites see Brittain et al. (2009a).

Point counts generally followed the methods established by Ralph et al. (1993). Thirty sampling points were located in each habitat type (150 total) in 2006 and 2007 (Brittain et al. 2009a). Ten-minute counts at each point were conducted twice, at least two weeks apart, within 4 hr of sunrise during the sampling period between 19 May and 9 June in 2006, and between 17 May and 13 June in 2007. During each 10-minute sampling event the relative distance was estimated within 5-m intervals from the sampling point for every bird detected except flyovers. The mean density of breeding birds was estimated for 23 PIF priority species using the program

Distance 5.0 (Thomas et al. 2006), as well as a 95% confidence interval. Detailed distance-sampling results are available in Brittain et al. (2009a).

GIS land use modeling

GIS raster data was obtained from the 1998 land cover map of Georgia (land cover map), based on 30x30-m Landsat TM imagery from 1996-1998, from the Natural Resource Spatial Analysis Laboratory (NARSAL) at the University of Georgia available at http://narsal.uga.edu/.

GIS raster datasets on the predicted effects of sea-level rise on spatial distribution of habitats were taken from Craft et al. (2009) in a 4110 km^2 region of coastal Georgia (Figure 1). Changes in habitat were modeled in response to accelerated sea-level rise using the "Sea-Level Affects Marshes Model" (SLAMM5; Park et al. 1989). SLAMM5 uses elevation-submergence and wave action-erosion parameters, salt-water intrusion in river-dominated estuaries based on freshwater discharge and estuary cross-sectional area, to simulate habitat loss in response to accelerated SLR (Craft et al. 2009). Simulations were based on the mean (52 cm) and maximum (82 cm) increase in SLR in the IPCC Special Report on Emissions Scenarios (SRES) assuming rapid economic growth, a mid-century population peak and rapid introduction of new and more efficient technologies with a balanced use of fossil and non-fossil fuels (A1B scenario; IPCC 2007). Model simulations were initiated beginning in 1999 and run to 2100 A.D.

Rates of urban development were estimated from the future land use plans of Liberty, Bryan, Chatham and McIntosh Counties in Georgia as part of the Georgia Coastal Comprehensive Plan available at http://www.georgiaplanning.com/coastal.htm (NOAA 2003). Other counties in Georgia did not give projected area or percent changes in land use types so we extrapolated from the available future land use plans to assume the same growth rates throughout the region. The average annual rates of planned increases in residential, commercial and industrial land uses ranged from 2.3% (industrial) to 2.9% (commercial) from 1999-2020 for

Liberty County and from 1990-2010 for all other counties. Based on these estimates, urban development was modeled for 2100 at rates of 1% and 2.5% annual growth. Urban land use classifications (low intensity urban, high intensity urban, and low intensity urban forests) were selected from the land cover map, reclassified as all urban habitat, converted to vector data, buffered and converted back to raster until the amount of urban areas were approximately the amount equal to the projected level of annual growth in 2100. There were approximately 65,102 hectares of urban land classes in 1998, projected to increase to ~179,000 hectares in 2100 assuming 1% annual growth of urban land uses, and ~808,000 hectares in 2100 assuming 2.5% annual growth. Modeling annual growth of urban areas from 1998 to 2100 in GIS required placing a 213.2 m buffer of urban land use around the existing 65,102 hectares of urban land use areas to increase their size to ~179,000 hectares to simulate 1% annual growth, and a 1541.7 m buffer for 2.5% annual growth. Projected increases in urban areas in response to 1% and 2.5% annual growth were added back to the land cover map, and these new raster files were added to the SLAMM5 maps from Craft et al. (2009), creating a matrix of 5 maps: 1) 1999 at mean A1B sea-level, 2) 2100 at mean A1B sea-level and 1% annual urban growth, 3) 2100 at maximum A1B sea-level and 1% annual urban growth, 4) 2100 at mean A1B sea-level and 2.5% annual urban growth, and 5) 2100 at maximum A1B sea-level and 2.5% annual urban growth.

An analysis of the relative importance of SLR and development to terrestrial habitat changes was conducted assuming tidal wetland areas would not be developed due to protections given in Section 404 of the Clean Water Act Section (33 USCS §§ 1251-1387). In terrestrial habitats, the relative importance of development was assessed by summing the estimated area of each habitat that was lost to urban development first, followed by losses due to SLR, assuming that humans would not interfere with the landward progression of the sea.

Gap analysis species-habitat associations were used to estimate the area of appropriate habitats for each species (Kramer et al. 2003). For species with no special patch size or edge requirements, the total area of each habitat type was calculated from raster files by multiplying the number of cells times the area of each cell (900 m^2). The final raster files were also converted to vector to allow selection of polygons to meet the special needs, such as minimum patch size, of four species using Gap methods (Table 1). Hooded Warblers (see Table 2 for scientific names) required forests > 15 ha, Northern Parula required forests > 30 ha, and Summer Tanagers required forest > 40 ha (Kramer et al. 2003). Acadian Flycatcher models were created by generating a 90-m buffer along major streams and selecting all appropriate forest types within that buffer that were also sampled in the study. The selected buffered forests were combined with all bottomland hardwood forests, including tidal forest, and any patch greater than 15 ha was kept for Acadian Flycatcher habitat (Kramer et al. 2003). Yellow-throated Vireos were modeled based on selecting all appropriate forest cells within 500 m of an edge cell in the original raster files (Kramer et al. 2003). Edge cells were determined by selecting cells of appropriate forest habitat that were adjacent to open habitat (utility swaths, clearcuts, pasture and coastal scrub). The total area and number of patches of habitat available to each of the five species are given in Table 1.

Population estimates for each species in each scenario were calculated by multiplying the total area of appropriate habitats by the 95% confidence interval of breeding density for each species in those habitats (Table 2). Actual breeding densities of each species in each habitat were assumed to lie somewhere between the upper and lower confidence limits during the modeled time interval.

RESULTS

Avian Habitat Areas

The baseline area of coastal Georgia habitats assuming A1B mean SLR in 1999, was 413.0 km^2, 1116.0 km^2, 9.7 km^2, 459.9 km^2 and 2003.7 km^2 of tidal forest, saltmarsh, shrub, oak and pine, respectively (Figure 2). In 2100, the mean A1B SLR and 1% annual urban growth model showed that shrub habitat decreased by the largest percent (43.1%), but the largest total change was in pine forest (374.4 km^2). Losses of oak due to urban development alone were similar to the losses due to SLR (Figure 2). Shrub-habitat losses were much greater due to SLR than urban development alone, but pine forest losses were moderately larger due to SLR. Among wetland habitats, saltmarsh lost the greatest area (506.0 km^2) and tidal forest had the largest percent loss (23.5%; Figure 3).

Models for 2100 based on maximum A1B SLR and 1% annual urban growth rates also demonstrated that shrub decreased by both the largest percent (50.5%) and pine forest lost the greatest total area (407.9 km^2). Habitat losses due to urban development alone versus SLR showed the same pattern as the mean A1B SLR and 1% annual urban growth models, shrub habitat exhibited the greatest percent decline and pine forest the largest absolute decline (Figures 2 & 3).

Annual urban growth models at 2.5% for 2100 with either mean or maximum A1B SLR showed that oak forest had the largest percent losses (73.7 and 74.7%, respectively) but pine forest had the largest total area losses (1294.3 km^2 and 1250.8 km^2, respectively). However, oak and pine forest losses occurred primarily from urban development, whereas shrub losses were primarily due to SLR (Figure 2).

Gap analysis methods showed very little Acadian Flycatcher habitat in oak or pine forest in 1999 (0.2 km^2 each), but tidal forest had 379.5 km^2 in 160 patches (Table 1). By 2100, oak forest habitat for Acadian Flycatchers disappeared in all scenarios, whereas pine forest habitat disappeared with 2.5% annual urban growth while tidal forest habitat maintains at least 100 patches totaling 239.1 km^2. Yellow-throated Vireo edge habitat was largest in pine forest in all scenarios, but decreased by 65.0% in the worst-case scenario (maximum SLR with 2.5% annual urban growth). Also under the worst-case scenario, Yellow-throated Vireo habitat in oak forest decreased up to 77.6%. Northern Parula habitat in pine forest decreased by 66.8%, whereas tidal forest habitat decreased by 37.4%. Appropriate shrub habitat for Northern Parula is predicted to decrease to 1 patch totaling 0.7 km^2 by 2100. Hooded Warblers had 160 patches in tidal forest in 1999 (379.5 km^2), decreasing in area by 37.0% (100 patches) by 2100. Summer Tanager habitat showed the same pattern as Northern Parula with most habitat available in pine forest, but that decreased at a more rapid rate than tidal forest (Table 2).

Avian Populations

Tidal forest was the most important habitat for Yellow-crowned Night Heron, Yellow-billed Cuckoo and Prothonotary Warbler in 1999 (451 - 2,154, 10,195 - 34,872 and 15,863 - 27,940, respectively) and in 2100 under any scenario (Table 3). Hooded Warblers also depended most on tidal forest due primarily to their greater density in this habitat (12,177 - 35,545 in 1999), whereas Acadian Flycatchers were mostly in tidal forest due to the large area of this preferred habitat (31,535 - 57,574 in 1999). Saltmarsh was the most important habitat for Great Blue Heron, Great Egret, Clapper Rail and Seaside Sparrow in 1999 (492 - 6,411, 2,789 - 13,858, 65,184 - 182,087 and 5,829 - 35,959, respectively) and any scenario for 2100.

Shrub habitat contained the most Orchard Orioles in 1999 (73 - 808) and all scenarios for 2100, even though it covers a small portion of the coastal Georgia landscape. Shrub habitat populations of all species were < 1,485 due to the small extent of shrub habitat across the landscape. Similarly, despite having Eastern Wood-Pewee, White-eyed Vireo, Yellow-throated Vireo, Northern Parula and Yellow-throated Warbler as indicator species (Brittain et al. 2009a), oak forest only had the most abundant populations of White-eyed Vireos in 1999 (65,728 - 94,666) . However, pine forest could potentially have more White-eyed Vireos than oak forest in 2100 (Table 3)

Pine forest was the most important habitat for preserving the largest numbers of Red-headed Woodpeckers (22,243 - 69,168), Eastern Wood-Pewees (63,666 - 124,477), Yellow-throated Vireos (96,816 - 307,111), Carolina Chickadees (130,173 - 330,572), Brown-headed Nuthatches (941,524 - 1,512,982), Northern Parula (57,399 - 124,508), Yellow-throated Warblers (166,863 - 268,718), Pine Warblers (190,755 - 313,040), Yellow-breasted Chat (12,744 - 69,218), Summer Tanager (17,374 - 39,393), Eastern Towhee (76,023 - 161,034) and Painted Bunting (20,021 - 74,262) in 1999 (Table 3). Pine forest continues to have the greatest numbers for these species in 2100, except for Summer Tanager, for which, under the worse-case scenario of maximum SLR and 2.5% annual growth, tidal forest may become more important (6,438 - 14,234). Due to their high density and the large area of pine forest, Brown-headed Nuthatches in pine forest had the largest population of all species in all habitats in 1999 and each of the scenarios for 2100. Acadian Flycatchers had the smallest population total for pine forest (4-11 birds in 1999), since they were modeled using only forest patches > 15 hectare within 90 m of streams (Kramer et al. 2003).

DISCUSSION

Avian Habitat Areas

Predicted changes in habitat due to urban development and SLR represent our best estimate but our predictions contain considerable uncertainties in projected rates of SLR and development along the Georgia coast. Maximum annual urban growth rates were based on predicted increases within the region at 2.5% per year from about 2000 to 2020, which seems unsustainable over the coming century. Another uncertainty is that urban growth models do not account for asymmetrical growth.

Changes in habitat due to SLR based on SLAMM5 also have uncertainty because of the coarse resolution of the elevation data and lack of feedback mechanisms, such as increased macrophytic production and sediment deposition with increased sea-level or increased decomposition of soil organic matter in tidal forests with saltwater intrusion in the model (Craft et al. 2009). Predicted rates of SLR are also the focus of considerable uncertainties.

The relative importance of development versus SLR to habitat loss in coastal Georgia varies among habitats. SLR is the dominant threat to habitat loss for saltmarsh and tidal forest, but tidal forest will lose a higher percentage of area under the mean SLR scenario, whereas saltmarsh will lose more under the maximum SLR scenario. SLR is also the major threat to maritime shrub habitat. Urban development threatens to destroy a higher percentage of the oak forest habitat than pine forest (up to 55% vs. 50%). However, SLR and development are relatively equal threats to oak forest as long as development rates remain moderate (1% annually). Pine forests are slightly more threatened by SLR (up to 13%) than urban growth (8%) as long as growth remains moderate (1% annually).

Our predictions suggest Acadian Flycatchers are likely to decline or disappear from oak forest lost primarily to development and pine forests lost to SLR and development. However, 28 Acadian Flycatchers were detected in oak forest and 13 in pine forest during the study period, both more than predicted using Gap analysis species-habitat associations (Brittain et al. 2009a). Models using Gap species-habitat associations also showed that declines in Northern Parula, Hooded Warbler and Summer Tanager populations were less in tidal forest than oak and pine forest, suggesting that tidal forests may serve as refuges for these species by 2100. Yellow-throated Vireos, in contrast, are dependent on pine forests for the largest portion of their population in every scenario.

The PIF Conservation Plans for coastal Georgia habitats rely on maintaining “largely forested areas with some edge and forest openings for (Painted) buntings,” with a focus on “structural diversity of (tidal forest) woodlands,” and emphasis on late successional stands in pine forest with increasing disturbance regimes (Hunter et al. 2001). These plans appear to be appropriate given the predicted changes due to SLR and development in this study. Late successional pine stands with well-developed understories, as recommended by PIF, support Brown-headed Nuthatches and Red-headed Woodpeckers, as well as Painted Buntings and Eastern Towhees.

Avian Populations

Tidal forests contain the largest population of Yellow-crowned Night Herons, Yellow-billed Cuckoos, Acadian Flycatchers, Prothonotary Warblers and Hooded Warblers (Table 3), but the only species unique to them (Brittain et al. 2009a) was the moderate-priority Prothonotary Warbler (Hunter et al. 2001). Estimates of Seaside Sparrow populations, which are especially needed for PIF conservation plans (Hunter et al. 2001) range between 5,829 and 35,959 in coastal Georgia in 1999.

While Painted Buntings and Eastern Towhees had higher densities in shrub habitat (Dickinson 1952, Robertson and Woolfenden 1992, Brittain et al. 2009a), their populations are higher in the larger oak and pine forests of coastal Georgia, that buffer them against SLR assuming limited urban development. The small area of shrub habitat, limits its utility as a significant repository of any avian species. Because of their large area, pine forests had the greatest population sizes of most PIF priority species (14), including the PIF extremely high priority Painted Bunting (Hunter et al. 2001). Logging activity is higher in pine forests in this region. Thus, oak and tidal forests may provide refuge from SLR and development for species that require undisturbed, mature forest patches, including Acadian Flycatcher, Northern Parula and Yellow-throated Warbler (Sprunt 1953, Moldenhauer and Regelski 1996, Whitehead and Taylor 2002).

Species Threats

Painted Bunting populations are especially susceptible to the decline in shrub habitats because of their strong preference for this habitat. Pine forests, though, may provide refuges for this species. Saltmarsh is also important for Painted Buntings as Brittain et al. (2009b) suggested that this habitat contributes almost as much food to their diet as terrestrial sources. Similarly, Eastern Towhees, White-eyed Vireos and Yellow-breasted Chats will be adversely affected by declining shrub habitat, but may be able to find refuge in early successional oak and pine forests.

The greatest threat to most terrestrial species is urban development that leads to the loss of ~49% pine and ~54% oak forest. Red-headed Woodpeckers, Brown-headed Nuthatches and Pine Warblers that have higher densities in pine forest are threatened not only from development but also logging activities that destroy the mature pines necessary for breeding activities (Hamel 1992, Rodewald et al. 1999). Edge species such as Eastern Wood-Pewee, Yellow-throated Vireo, Carolina Chickadee and Summer Tanager may benefit from logging activities that maintain pine and oak forest openings, whereas closed-canopy species such as Acadian Flycatcher, Northern Parula, Yellow-throated Warbler will need patches of mature oak to maintain healthy populations. Tidal forest may also provide habitat for Acadian Flycatchers, Carolina Chickadees, Northern Parula and Summer Tanagers as to oak and pine forest is lost to development.

CONCLUSIONS

In coastal Georgia, avian habitats are differentially threatened in the coming century by the processes of urban development and SLR. Wetland habitats, such as saltmarsh and tidal forest, in addition to maritime shrub habitat, are under greater threat from SLR than from development. Tidal forests may also serve as refuges for closed-canopy species that lose oak and pine forests to development. Shrub habitat is so rare in coastal Georgia that any loss may have a greater impact on shrub-associated species than declines in other wetland and terrestrial habitats. It will be important to maintain suitable open-canopy oak and pine forests as refuge for shrub-associated species as shrub habitat disappears. Urban development threatens oak and pine forests, especially under accelerated development scenarios (2.5% annually).

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TABLE 1. Estimated suitable habitat area (km^2) and number of patches (in parentheses) for species with specific requirements in coastal Georgia for 1999 and 2100.

Species	Habitat	1999	2100 A1B mean - 1%	2100 A1B max - 1%	2100 A1B mean - 2.5%	2100 A1B max - 2.5%
Acadian Flycatcher	oak forest	0.2 (1)	0	0	0	0
	pine forest	0.2 (1)	0.2 (1)	0.2 (1)	0	0
	tidal forest	379.5 (160)	283.2 (126)	283.2 (126)	239.1 (100)	239.1 (100)
Yellow-throated Vireo*	oak forest	416	246.5	237.6	97.1	93.3
	pine forest	1858.4	1476.6	1441.8	664.6	649.8
Northern Parula	oak forest	126.1 (188)	77.0 (117)	70.6 (109)	34.6 (48)	30.4 (43)
	pine forest	1038.8 (1556)	827.2 (1254)	799.6 (1207)	390.5 (575)	345.0 (556)
	shrub	1.6 (3)	0.7 (1)	0.7 (1)	0.7 (1)	0.7 (1)
	tidal forest	368.6 (108)	273.3 (78)	273.3 (78)	230.7 (60)	230.7 (60)
Hooded Warbler	oak forest	170.8 (406)	106.9 (260)	98.9 (244)	49.8 (120)	45.6 (116)
	tidal forest	379.5 (160)	283.2 (126)	283.2 (126)	239.1 (100)	239.1 (100)
Summer Tanager	oak forest	102.4 (119)	60.3 (68)	55.4 (65)	27.8 (28)	23.4 (23)
	pine forest	879.3 (1096)	694.9 (872)	674.1 (845)	328.5 (396)	279.7 (367)
	shrub	1.6 (3)	0.7 (1)	0.7 (1)	0.7 (1)	0.7 (1)
	tidal forest	362.4 (91)	269.8 (68)	269.8 (68)	229.3 (56)	229.3 (56)

* Yellow-throated Vireos require forest within 500 m of an edge, not a specific patch size

TABLE 2. Projected range of avian population numbers in five habitats of coastal Georgia in 1999 and 2100.

Habitat	Species *(Scientific name)*	1999	2100 A1B mean - 1%	2100 A1B max - 1%	2100 A1B mean - 2.5%	2100 A1B max - 2.5%
oak forest	Red-headed Woodpecker *(†Melanerpes erythrocephalus)*	1228 - 6583	766 - 4109	737 - 3952	323 - 1733	311 - 1667
	Eastern Wood-Pewee *(*Contopus virens)*	13293 - 25580	8298 - 15968	7981 - 15358	3500 - 6735	3367 - 6479
	Acadian Flycatcher *(*Empidonax virescens)*	10 - 20	0 - 0	0 - 0	0 - 0	0 - 0
	White-eyed Vireo *(†Vireo griseus)*	65728 - 94666	41029 - 59093	39461 - 56835	17305 - 24924	16648 - 23977
	Yellow-throated Vireo *(*Vireo flavifrons)*	10312 - 27166	5888 - 15512	6110 - 16096	2311 - 6089	2407 - 6342
	Carolina Chickadee *(†Poecile carolinensis)*	33751 - 90062	21068 - 56219	20263 - 54071	8886 - 23712	8549 - 22811
	Brown-headed Nuthatch *(††Sitta pusilla)*	15681 - 46167	9788 - 28819	9414 - 27718	4128 - 12155	3972 - 11693
	Northern Parula *(††Parula Americana)*	21998 - 39898	12325 - 22355	13433 - 24364	5304 - 9619	6037 - 10950
	Yellow-throated Warbler *(††Dendroica dominica)*	59841 - 91483	37354 - 57106	35927 - 54924	15755 - 24086	15157 - 23171
	Pine Warbler *(†Dendroica pinus)*	17479 - 36168	10911 - 22577	10494 - 21715	4602 - 9523	4427 - 9161
	Hooded Warbler *(††Wilsonia citris)*	275 - 3532	159 - 2044	172 - 2211	73 - 944	80 - 1030
	Summer Tanager *(*Piranga rubra)*	2286 - 5769	1237 - 3122	1346 - 3396	523 - 1320	621 - 1568
	Eastern Towhee *(†Pipilo erythhrophthalmus)*	1907 - 13530	1190 - 8445	1145 - 8123	502 - 3562	483 - 3427
	Painted Bunting *(‡Passerina ciris)*	3175 - 12294	1982 - 7674	1906 - 7381	836 - 3237	804 - 3114
pine forest	Red-headed Woodpecker	22243 - 69168	18088 - 56245	17715 - 55087	7876 - 24491	8358 - 25990
	Eastern Wood-Pewee	63666 - 124477	51771 - 101221	50705 - 99136	22542 - 44074	23922 - 46772
	Acadian Flycatcher	4 - 11	4 - 11	4 - 11	0 - 0	0 - 0
	White-eyed Vireo	27986 - 88776	21713 - 68876	22237 - 70538	9786 - 31042	10007 - 31745

	Yellow-throated Vireo	96816 - 307111	89935 - 285284	89411 - 283622	66537 - 211062	66315 - 210360
	Carolina Chickadee	130173 - 330572	105853 - 268812	103673 - 263275	46091 - 117047	48912 - 124212
	Brown-headed Nuthatch	941524 - 1512982	765619 - 1230313	749850 - 1204971	333369 - 535708	353776 - 568501
	Northern Parula	57399 - 124508	44180 - 95835	45710 - 99152	21575 - 46800	19066 - 41357
	Yellow-throated Warbler	166863 - 268718	135688 - 218513	132893 - 214012	59082 - 95146	62699 - 100970
	Pine Warbler	190755 - 313040	155117 - 254555	151922 - 249312	67541 - 110839	71670 - 117624
	Yellow-breasted Chat *(*Icteria virens)*	12774 - 69218	10388 - 56286	10174 - 55127	4523 - 24508	4800 - 26009
	Summer Tanager	17374 - 39393	13320 - 30200	13731 - 31133	6492 - 14719	5526 - 12529
	Eastern Towhee	76023 - 161034	61820 - 130948	60546 - 128251	26918 - 57018	28565 - 60508
	Painted Bunting	20021 - 74262	16280 - 60387	15945 - 59143	7089 - 26294	7523 - 27904
saltmarsh	Great Blue Heron *(*Ardea Herodias)*	492 - 6411	392 - 5113	269 - 3504	392 - 5113	269 - 3504
	Great Egret *(*Ardea alba)*	2789 - 13858	2224 - 11052	1524 - 7575	2224 - 11052	1524 - 7575
	Clapper Rail *(††Rallus longirostris)*	65184 - 182087	51984 - 145212	35629 - 99528	51984 - 145212	35629 - 99528
	Seaside Sparrow *(††Ammodramus maritimus)*	5829 - 35959	4649 - 28677	3186 - 19655	4649 - 28677	3186 - 19655
shrub	White-eyed Vireo	922 - 1485	524 - 845	456 - 734	365 - 589	321 - 517
	Carolina Chickadee	387 - 1315	220 - 748	192 - 650	154 - 521	135 - 458
	Brown-headed Nuthatch	200 - 1077	114 - 613	99 - 532	79 - 427	70 - 375
	Northern Parula	6 - 33	3 - 14	3 - 14	3 - 14	3 - 14
	Yellow-throated Warbler	116 - 403	66 - 229	58 - 199	46 - 160	40 - 140
	Pine Warbler	315 - 678	179 - 386	156 - 335	125 - 269	110 - 236
	Yellow-breasted Chat	280 - 807	159 - 459	138 - 399	111 - 320	97 - 281
	Summer Tanager	15 - 47	7 - 21	7 - 21	7 - 21	7 - 21

	Eastern Towhee	841 - 1435	478 - 816	416 - 710	333 - 569	293 - 500
	Painted Bunting	516 - 1018	294 - 579	255 - 503	205 - 404	180 - 354
	Orchard Oriole *(†Icterus spurious)*	73 - 308	41 - 175	36 - 153	29 - 122	25 - 107
tidal forest	Yellow-crowned Night Heron *(*Nyctanassa violacea)*	451 - 2154	345 - 1648	292 - 1392	345 - 1648	292 - 1392
	Yellow-billed Cuckoo *(†Coccyzus americanus)*	10195 - 34872	7801 - 26682	6591 - 22544	7801 - 26682	6591 - 22544
	Acadian Flycatcher	31535 - 57574	19872 - 36280	23529 - 42958	19872 - 36280	23529 - 42958
	White-eyed Vireo	4754 - 16014	3638 - 12253	3074 - 10353	3638 - 12253	3074 - 10353
	Carolina Chickadee	16627 - 64040	12722 - 48999	10749 - 41401	12722 - 48999	10749 - 41401
	Northern Parula	22099 - 44751	13831 - 28008	16386 - 33182	13831 - 28008	16386 - 33182
	Prothonotary Warbler *(†Protonotaria citrea)*	15863 - 27940	12137 - 21378	10255 - 18063	12137 - 21378	10255 - 18063
	Hooded Warbler	12177 - 35545	7674 - 22398	9086 - 26521	7674 - 22398	9086 - 26521
	Summer Tanager	8647 - 19117	5470 - 12093	6438 - 14234	5470 - 12093	6438 - 14234

Estimated by multiplying the area of habitat in each scenario by the 95% confidence interval of breeding bird density for each species.

* = species of local or regional interest, *†* = species of moderate priority, *††* = species of high priority, and *‡* = species of extremely high priority.

FIG. 1. Map of SLR and urban development study area in coastal Georgia.

FIG. 2. Total area of terrestrial habitats in coastal Georgia in 1999 and area lost to development and SLR in 2100 as modeled in different scenarios of sea-level rise (SLR; A1B mean and A1B max) and annual urban growth rates (1% and 2.5%).

FIG. 3. Total area of wetland habitats in coastal Georgia in 1999 and 2100 as modeled in different scenarios of sea-level rise (SLR; A1B mean and A1B max). Taken from Craft et al. (2009).

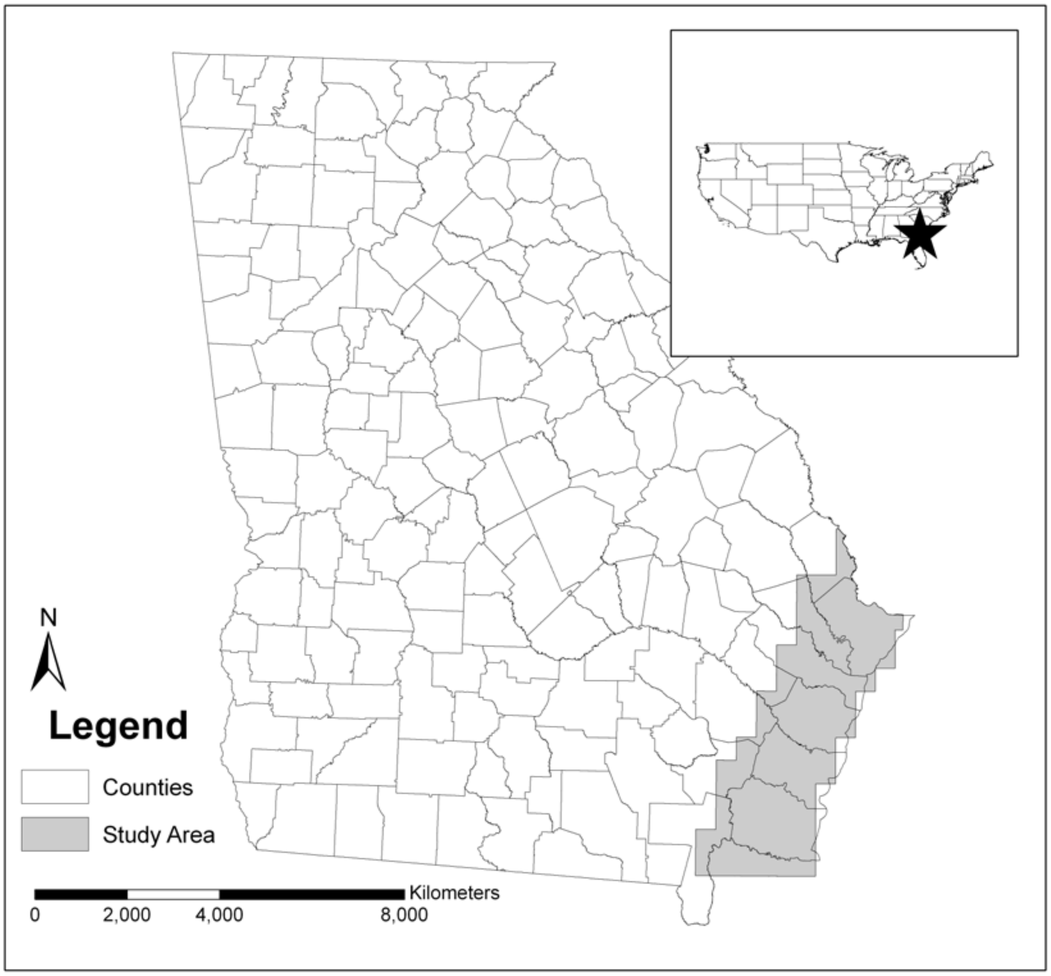
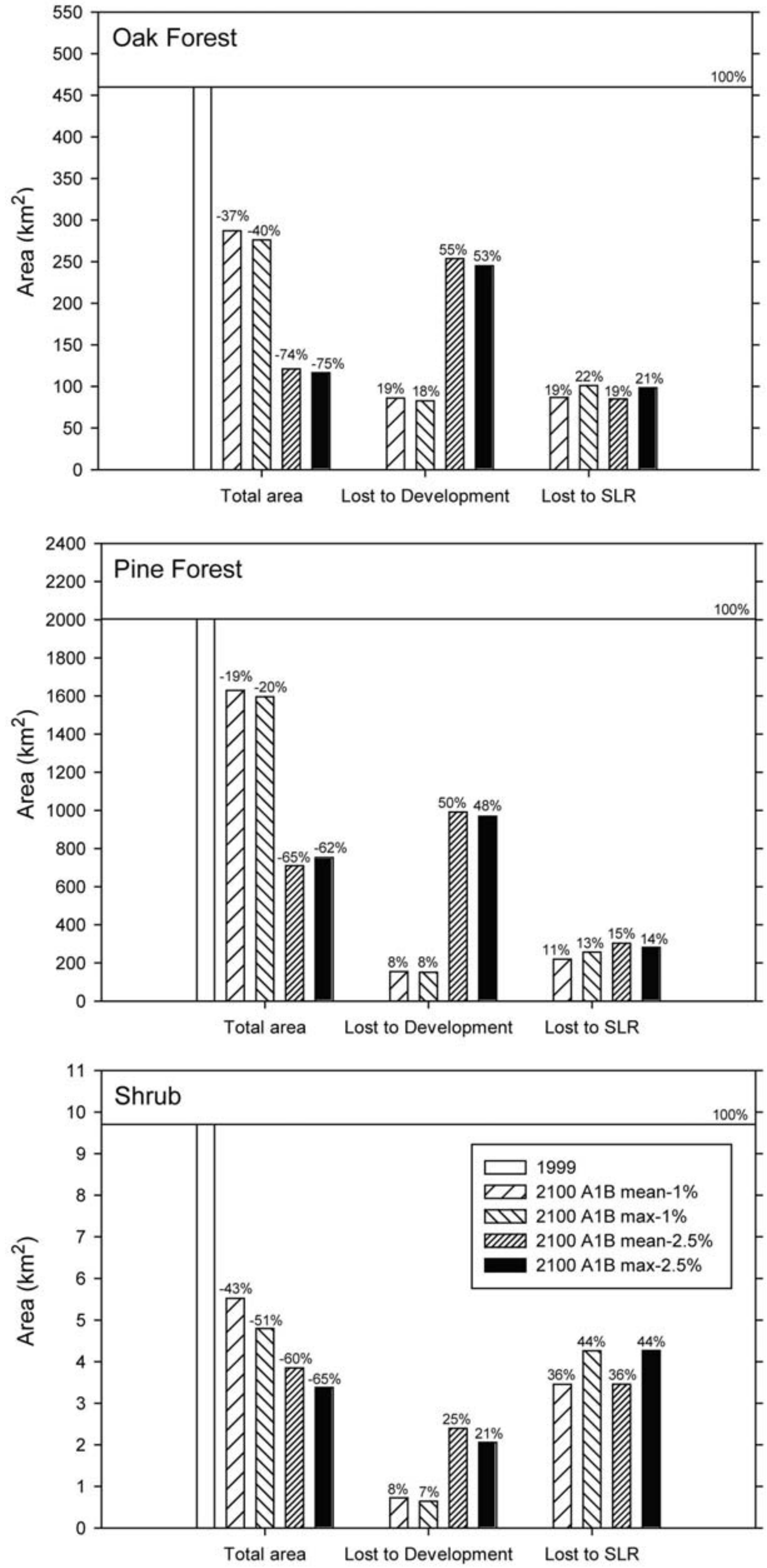


Figure 1.



Oak Forest
Pine Forest
Shrub
Area (km²)
100%
Total area
Lost to Development
Lost to SLR
-37%
-40%
-74%
-75%
19%
18%
55%
53%
19%
22%
19%
21%
-19%
-20%
-65%
-62%
8%
8%
50%
48%
11%
13%
15%
14%
-43%
-51%
-60%
-65%
8%
7%
25%
21%
36%
44%
36%
44%
1999
2100 A1B mean-1%
2100 A1B max-1%
2100 A1B mean-2.5%
2100 A1B max-2.5%

Figure 2.

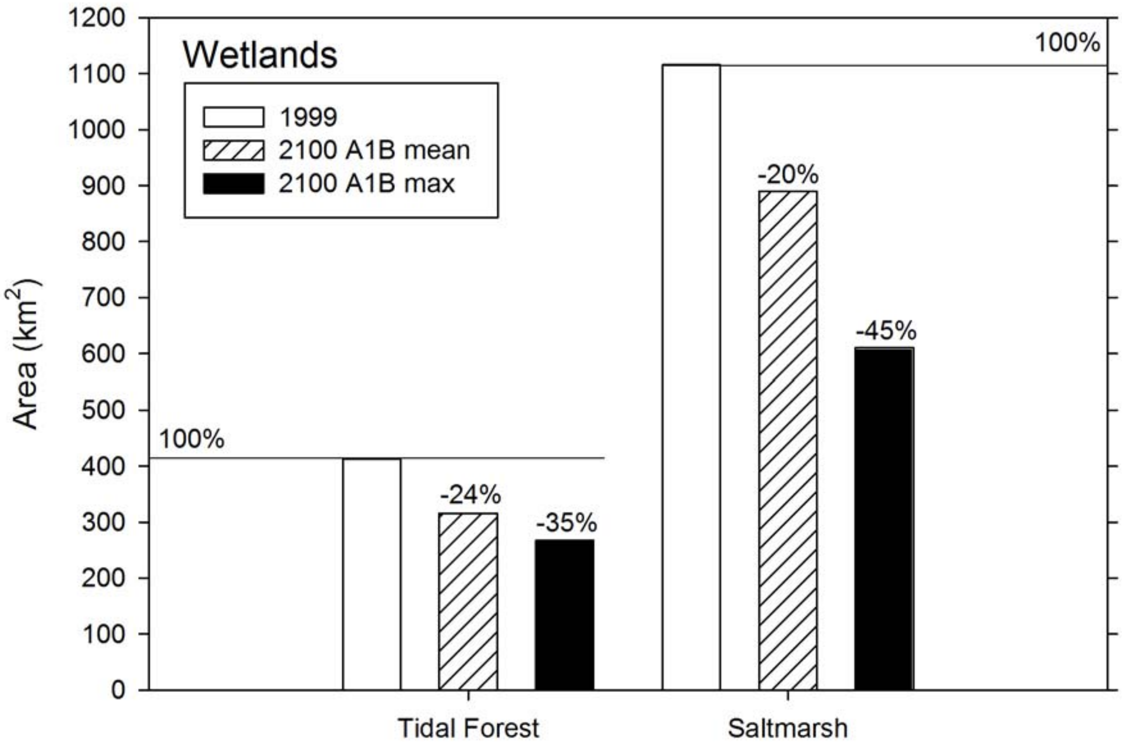

Wetlands
1999
2100 A1B mean
2100 A1B max
Area (km^2)
100%
-24%
-35%
100%
-20%
-45%
Tidal Forest
Saltmarsh
0
100
200
300
400
500
600
700
800
900
1000
1100
1200

Figure 3.

APPENDIX. Appropriate habitats and GAP analysis method for species analyzed in coastal Georgia. Modified from Kramer et al. 2003.

Species	Habitats	Buffered habitats	Buffer	Mask
Great Blue Heron	Saltmarsh = 920.	-	-	-
Great Egret	Saltmarsh = 920.	-	-	-
Yellow-crowned Night Heron	Tidal forest = 890 & 900.	-	-	-
Clapper Rail	Saltmarsh = 920.	-	-	-
Yellow-billed Cuckoo	Tidal forest = 890 & 900.	-	-	-
Red-headed Woodpecker	Oak forest = 412, 420 & 434. Pine forest = 441 & 990.	-	-	-
Eastern Wood-Pewee	Oak forest = 412, 420 & 434. Pine forest = 441 & 990.	-	-	-
Acadian Flycatcher	Tidal forest = 890 & 900. Oak forest = 412, 420 & 434. Pine forest = 441 & 990.	890, 412, 420, 434, 441 & 990	Within 90 m of stream	All >15 ha
White-eyed Vireo	Tidal forest = 890 & 900. Oak forest = 412, 420 & 434. Pine forest = 441 & 990. Shrub = 9 & 513.	-	-	-
Yellow-throated Vireo	Oak forest = 412, 420 & 434. Pine forest = 441 & 990.	*		
Carolina Chickadee	Tidal forest = 890 & 900. Oak forest = 412, 420 & 434. Pine forest = 441 & 990. Shrub = 9 & 513.	-	-	-
Brown-headed Nuthatch	Oak forest = 412, 420 & 434. Pine forest = 441 & 990. Shrub = 9 & 513.	-	-	-
Northern Parula	Tidal forest = 890 & 900. Oak forest = 412, 420 & 434. Pine forest = 441 & 990. Shrub = 9 & 513.	-	-	All >30 ha

Yellow-throated Warbler	Oak forest = 412, 420 & 434. Pine forest = 441 & 990. Shrub = 9 & 513.	-	-	-
Pine Warbler	Oak forest = 412, 420 & 434. Pine forest = 441 & 990. Shrub = 9 & 513.	-	-	-
Prothonotary Warbler	Tidal forest = 890 & 900.	-	-	-
Hooded Warbler	Tidal forest = 890 & 900. Oak forest = 412, 420 & 434.	-	-	All >15 ha
Yellow-breasted Chat	Pine forest = 441 & 990. Shrub = 9 & 513.	-	-	-
Summer Tanager	Tidal forest = 890 & 900. Oak forest = 412, 420 & 434. Pine forest = 441 & 990. Shrub = 9 & 513.	-	-	All >40 ha
Eastern Towhee	Oak forest = 412, 420 & 434. Pine forest = 441 & 990. Shrub = 9 & 513.	-	-	-
Seaside Sparrow	Saltmarsh = 920.	-	-	-
Painted Bunting	Oak forest = 412, 420 & 434. Pine forest = 441 & 990. Shrub = 9 & 513.	-	-	-
Orchard Oriole	Shrub = 9 & 513.	-	-	-

* = Yellow-throated Vireo habitat was selected by masking an area created from a grid of edge cells between the forested habitats noted above and any cell with open habitat (20 = Utility Swath, 31 = Clearcut – Sparse Vegetation, 80 = Pasture, Hay, and 513 = Coastal Scrub), applying a 1 km moving window (FOCALMEAN using rectangle) and keeping the areas with values > 0.

Habitat key: 9 = Coastal Dune, 412 = Hardwood Forest, 420 = Live Oak, 434 = Mixed Pine-hardwood, 441 = Loblolly-Slash Pine, 513 = Coastal Scrub, 890 = Cypress-Gum Swamp, 900 = Bottomland Hardwood, 920 = Saltmarsh, and 990 = Evergreen Forested Wetland.

Ross A. Brittain
Curriculum Vitae

EDUCATION

2005- 2009 Indiana University, Bloomington – PhD in Environmental Science (defended 4/3/2009), GPA = 4.0

Dissertation research: Determining avian population densities in coastal Georgia and modeling the likely effects of sea level rise on avian populations of coastal Georgia using GIS techniques. Characterizing avian trophic webs for Clapper Rail, Marsh Wren, Northern Parula, Yellow-throated Warbler, Carolina Wren, Painted Bunting, White-eyed Vireo, Brown-headed Nuthatch, Red-bellied Woodpecker and Eastern Screech Owl by comparing their C and N isotopic signals to primary producers and invertebrates.

2003-2006 Indiana University, Bloomington – Masters in Environmental Science (MSES, Applied Ecology) and Masters in Public Affairs (MPA, Natural Resource Management), GPA = 4.0

1985-1990 Indiana University, Bloomington – BA in Fine Arts, Studio, GPA = 3.85

EXPERIENCE

2009-present *Environmental Manager*, Indiana Department of Environmental Management. Perform risk assessment for State Cleanup, Voluntary Remediation Program and Leaking Underground Storage Tank Project Managers.

2007-2008 *Consultant Assistant*, U.S. Department of Justice for US v Rapanos court case. Assist Dr. Chris Craft in the clarification of the definition of "significant nexus" connecting wetlands to navigable waters of the U.S. My primary responsibilities were field sampling for wetland delineation and using GIS to estimate "similarly situated" wetlands within the watershed.

2005-2008 *Wetlands Lab Manager*, School of Public and Environmental Affairs, Indiana University, Bloomington. Supervise the laboratory procedures as part of Dr. Chris Craft's study of the impact of climate change (e.g. sea level rise) on wetland ecosystem functions and services across a salinity gradient in the Satilla, Ogechee and Altamaha river systems of coastal Georgia. Laboratory procedures included measuring total P using colorimetric techniques, measuring C and N using an Elemental Analyzer, and measuring soil accretion rates using Cs-137 and Pb-210 methods.

2004-2008 *Adjunct Faculty*, School of Public and Environmental Affairs, Indiana University, Bloomington. Principal instructor for E527 Applied Ecology and E440 Wetlands Biology and Regulation

2004 *Research Assistant*, JC Randolph Forest Ecology Laboratory, School of Public and Environmental Affairs, Indiana University, Bloomington (summer). Responsible for collecting soil samples, taking dendrology measurements and sorting fine roots for a study of carbon dynamics in a mid-latitude temperate forest ecosystem.

2004 *Field Ornithologist/Trail Designer*, Sycamore Land Trust, Bloomington, Indiana (summer). Design and conduct a point count survey of bird populations on the principal properties of the Sycamore Land Trust. Also designed a 1.5 mile environmental education trail and boardwalk in a 900-acre bottomland hardwood forest of Monroe County, Indiana.

2003-2004 *Intern*, Bloomington Environmental Commission, City of Bloomington Planning Department. Research green building design, green zoning ordinances and urban vegetation recommendations (focusing on non-native invasives) in preparation for rewriting the zoning ordinances for the City of Bloomington, Indiana.

2002-present *Coordinator*, Indiana Northern Saw-whet Owl Banding Stations, Sassafras Audubon Society, Bloomington, Indiana. Created the first study of fall migration patterns of Northern Saw-whet Owls in Indiana. As the Master Bander for the project (#23484) I am responsible for coordinating 6 subpermittees and over 200 volunteers. I also collect, enter and submit the annual banding data to the Bird Banding Laboratory in Patuxent, MD, and analyze the data for publication.

1995-2002 *Owner*, Wild Birds Unlimited, Bloomington, Indiana specialty retail store. Own and manage a specialty retail store devoted to the hobbies of birdwatching and birdfeeding. Included the responsibilities of hiring, supervising and firing employees, marketing, purchasing and accounting.

PUBLICATIONS

Brittain, R.A. 2008. Characterizing Northern Saw-whet Owl (*Aegolius acadicus*) Winter Habitats in South-central Indiana. **Proceedings of the Indiana Academy of Science 117:71-80**.

***Accepted*:**

Brittain, R.A., V. Meretsky and J. Gwinn. Northern Saw-whet Owl (*Aegolius acadicus*) autumn migration magnitude and demographics in Southern Indiana. **Journal of Raptor Research**. *Accepted, with edits, on 11/7/08, projected publication in September of 2009.*

***In preparation*:**

Brittain, R.A., C. Craft, and V. Meretsky. Breeding densities and habitat relationships of avian species in coastal Georgia, USA, using distance-sampling and indicator species analysis. *In preparation for* **Journal of Field Ornithology.**

Brittain, R.A., A. Schimmelman, and C. Craft. Sensitivity Analysis of Avian Food Web Characterization Using Isosource and Stable Isotopes of ^{13}C and ^{15}N. *In preparation for* **Oecologia**.

Brittain, R.A., A. Schimmelman, and C. Craft. Elucidating avian food webs in coastal Georgia, USA, using stable isotopes of ^{13}C and ^{15}N. *In preparation for* **Ecological Applications**.

Brittain, R.A., V. Meretsky, and C. Craft. Stemming the Tide: Likely Effects of Sea Level Rise on Avian Communities in Coastal Georgia, USA. *In preparation for* **Conservation Biology**.

EXTERNALLY FUNDED RESEARCH

2003 Sassafras Audubon Society, *Owl Adoption Program*, Ongoing funding for conducting research on Northern Saw-whet Owls in southern Indiana. (Over $4000 to date)

2006 National Estuarine Research Reserve System Graduate Research Fellowship (funded by the National Oceanic and Atmospheric Administration); "Characterization of Avian Food Source, Trophic Structure, and Habitat Utilization on Sapelo Island, and Coastal GA Using Stable Isotopes of C and N." Funding period: June 2006-May 2009. Federal funds: $60,000 over 3 years.

INVITED SEMINARS

March, 2007 Ball State University, Department of Biology (invited by Wildlife Society). *Characterizing Winter Habitats and Fall Migration Patterns of Northern Saw-whet Owls (*Aegolius acadicus*) in Southern Indiana.*

March, 2007 Indiana University, School of Public and Environmental Affairs, Environmental Science and Policy Seminar. *Characterizing Winter Habitats and Fall Migration Patterns of Northern Saw-whet Owls (*Aegolius acadicus*) in Southern Indiana.*

April, 2007 Beckham Bird Club, Monthly Seminar. Louisville, Kentucky. *Characterizing Winter Habitats and Fall Migration Patterns of Northern Saw-whet Owls (*Aegolius acadicus*) in Southern Indiana.*

October, 2007 University of Indianapolis, Biology Department Seminar. *Characterizing Winter Habitats and Fall Migration Patterns of Northern Saw-whet Owls (*Aegolius acadicus*) in Southern Indiana.*

May, 2008 Indiana Audubon Society Spring Birding Festival. McCormick's Creek State Park, Spencer, Indiana. *Characterizing Winter Habitats and Fall Migration Patterns of Northern Saw-whet Owls (*Aegolius acadicus*) in Southern Indiana.*

March, 2009 Indiana University, School of Public and Environmental Affairs, Environmental Science and Policy Seminar. *Avian Food Webs and Likely Effects of Sea Level Rise in Coastal Georgia*.

March, 2009 Ohio Bird Banding Association, Toledo, Ohio. *Avian Food Webs and Likely Effects of Sea Level Rise in Coastal Georgia*.

MEMBERSHIP IN PROFESSIONAL SOCIETIES and COMMITTEES

Ecological Society of America
American Ornithologists' Union
Society of Wetland Scientists
The Sycamore Land Trust (Advisory Board since 2002)
Sassafras Audubon Society (Board of Directors from 1998-2002, Outings Coordinator 2000-2002)
Environmental Resources Advisory Council for Bloomington Parks and Recreation, Chair 1999-2005
Bloomington Economic Development Corporation, representing Sassafras Audubon Society 2002-2003
Bloomington Environmental Commission 2002-2005
School of Public and Environmental Affairs Dean Student Advisory Council, Indiana University

HONORS and AWARDS

National Estuarine Research Reserve System Graduate Research Fellowship 2006
Daniel Willard Wetlands Fellowship 2005, School of Public and Environmental Affairs, Indiana University
Melissa Laney Clark Fellowship 2004, School of Public and Environmental Affairs, Indiana University
Friend of the Environment Award, Wild Birds Unlimited 1997 & 2000
Meritorious Service Award, Sassafras Audubon Society and National Audubon Society
Master Bird Banding Permit #23484, Bird Banding Laboratory, USGS Patuxent Wildlife Research Center
Certified Interpretive Guide, National Association for Interpretation
Best Environmental Science Manuscript, School of Public and Environmental Affairs PhD Conference 2009

TEACHING EXPERIENCE

Fall 2008: Wetlands Biology and Regulation, SPEA E440, Indiana University, Course Instructor
Spring 2008: Applied Ecology, SPEA E527, Indiana University, Course Instructor
Spring 2007: Applied Ecology, SPEA E527, Indiana University, Course Instructor
Fall 2007: Wetlands Biology and Regulation, SPEA E440, Indiana University, Teaching Assistant
Fall 2006: Wetlands Biology and Regulation, SPEA E440, Indiana University, Teaching Assistant
Spring 2005: Applied Ecology, SPEA E527, Indiana University, Course Instructor
Restoration Ecology, SPEA E534, Indiana University, Teaching Assistant
Fall 2004: People and the Environment, SPEA E162, Indiana University, Course Instructor